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THE TIDAL SYSTEM OF LAKE MARACAIBO, VENEZUELA[1]

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ABSTRACT

The tides of the Lake Maracaibo system are attributable to a standing wave produced by tidal waves entering from the Gulf of Venezuela and their reflection from the head of the lake. A node for the semidiurnal constituents occurs in the northern part of the lake. An antinode for the semidiurnal constituents occurs in Tablazo Bay, and this antinode may be presumed to coincide with the node of the diurnal constituents.

When the dimensions of the basin and friction are taken into account by the step-by-step integration of finite difference equations for continuity and gravitational acceleration, estimates of tidal elevations and currents agree approximately with those observed.

The presence of significant rotary tidal currents in Lake Maracaibo or effects of the rotation of the earth on the tide is excluded.

The influence of the antinode in Tablazo Bay on sedimentation and on the exclusion of salt water from the lake are discussed.

In a study of the hydrography of Lake Maracaibo it became evident that the tide is an important factor in depositing marine sediments in its approaches and in controlling the salt content of its water. The tide of the lake is too small to be of practical importance, but along the channel leading from Maracaibo to the Gulf of Venezuela the tidal conditions are of great interest to navigation and have been under continuous observation, formerly by the Maracaibo Bar Survey and presently by the Instituto Nacional de Canalizaciones. The phenomena are apparently complex but yield to analysis by principles commonly applied to the tides in narrow embayments when the topography of the tidal basin is taken into account, it being shown that the effects of the rotation of the earth are negligibly small even in the broad basin of the lake. The situation is an example of the degree to which a standing tidal wave may become distorted by extreme variations in the dimensions of the channel without losing its fundamental characteristics.

The topography of the lake and its approaches is shown in Figure 1.

The tide in the Caribbean is mainly diurnal and at Aruba has a mean range at spring tides of 21 cm. In the Gulf of Venezuela the semidiurnal constituents of the Caribbean tide are greatly augmented by resonance with the result that at Zaparita Island at its southwestern extremity, where the tide has access to the lake, the tide is semidiurnal and has a mean range of 90 cm (Redfield 1958).

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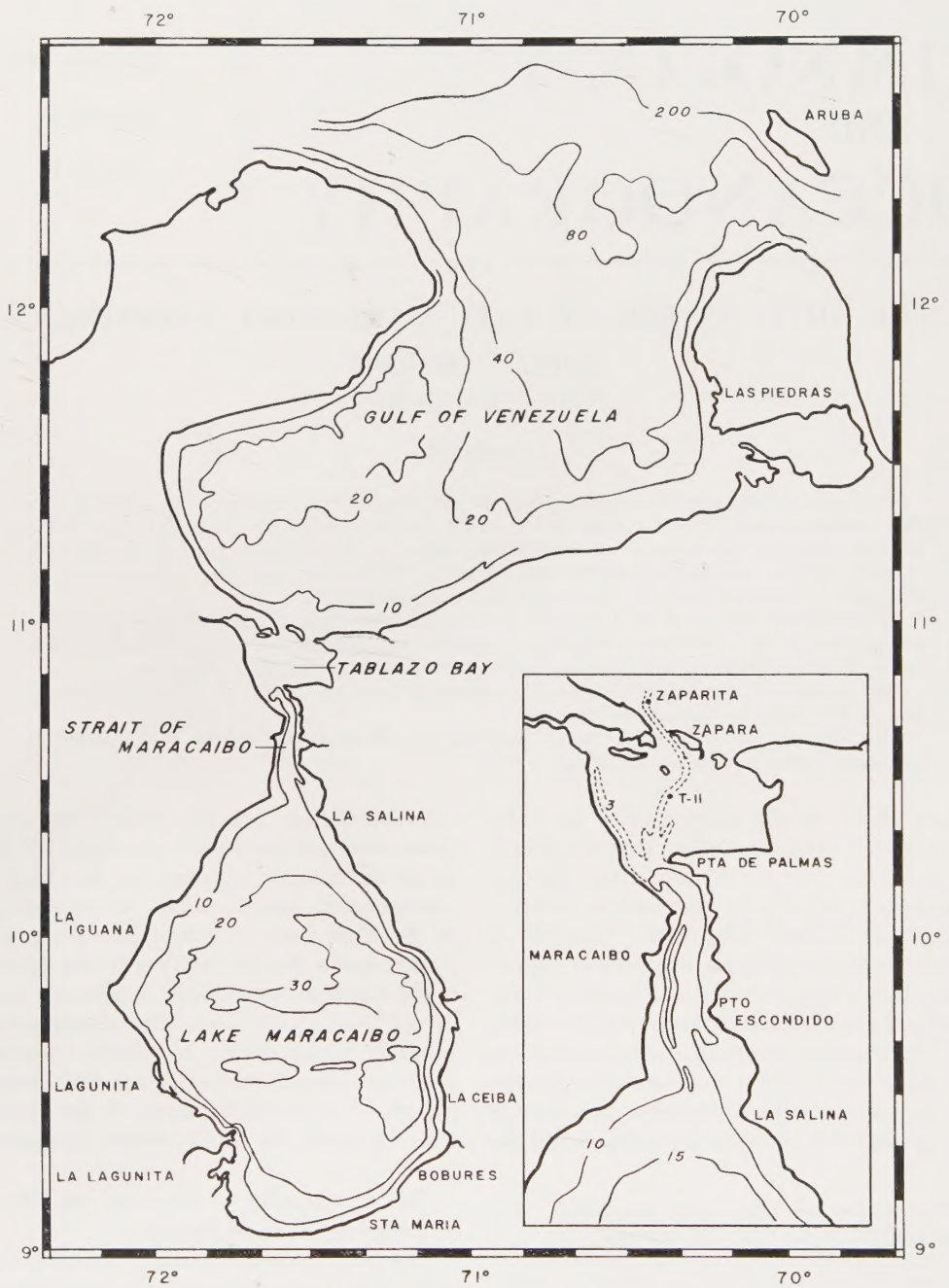

FIG. 1. Topography and place names of Lake Maracaibo and approaches.

Immediate access to the lake is by narrow and shallow channels across a barrier bar, and between barrier islands, and thence across Tablazo Bay to the Strait of Maracaibo. Tablazo Bay is shallow, the depths being reduced to some 2 m on the average by the deposition of sediments of marine origin (U. S. Waterways Experiment Station 1938). A dredged channel of 7-m depth across Tablazo Bay has been deep-

TABLE 1. *Harmonic constants*

	Constituent	Aruba 12°31′N 70°03′W	Zaparita 11°01′N 71°39′W	Zapara 10°58′N 71°34′W	Tablazo Bay 10°53′N 71°37′W	La Salina 10°23′N 71°28′W
Amplitude (H) cm						
	K_1	9.2	12.2	6.1	4.3	1.5
	O_1	6.1	9.2	3.1	2.4	0.4
	M_2	4.0	42.7	30.5	23.2	0.73
	S_2	2.1	3.1	3.1	3.1	—
Epoch (G)						
	K_1	241	251	247	247	021
	O_1	228	242	246	250	029
	M_2	161	269	284	296	287
	S_2	084	184	216	220	—

ened to 12 m since the present study was made. In contrast, the Strait of Maracaibo is a narrow trough 10 to 20 m deep extending some 20 km to widen into the lake. Lake Maracaibo is a broad shallow basin, unbroken by irregular physical features, which is some 85 km in length with a mean depth of 24 m and maximum depth of 35 m.

The tide retains its semidiurnal character across Tablazo Bay and along the Strait of Maracaibo. Along this stretch, after some delay in the entrance passages, high water is very nearly synchronous but the range of tide diminishes progressively lakeward. The relations of current to tidal elevation in the entrance passages is similar to that usually found in the inlets through barrier islands, the current flowing lakeward while the tide is rising (U. S. Waterways Experiment Station 1938). In the strait, in contrast, the current flows seaward at that time.

At the northern end of the lake the range of tide is greatly reduced. Spring tides appear to be diurnal, while semidiurnal components are evident during neap tides. At the southern end the semidiurnal character of the tide is restored and the range is increased to about 6 cm. High water occurs about 6 hr after high water in the Gulf of Venezuela.

Tides in embayments can usually be attributed to standing waves resulting from the interference of primary progressive waves entering from the outer sea and reflected waves engendered when the preceding primary wave is reflected from the head of the basin (Defant 1919). The varied tidal relations observed in the Maracaibo system may be explained quantitatively on this basis if the dimensions of the basin are taken into account. It can be shown that for the semidiurnal constituents a node exists in the northern part of the lake and that an antinode is present in Tablazo Bay. For the diurnal constituents a node is presumably present at the latter position.

DATA

The available harmonic analyses are given in Table 1. The constants for Aruba, Zaparita, Zapara and Tablazo Bay are from the Admiralty Tide Tables. The analysis for La Salina was made by Mr. A. R. Miller from records of Creole Petroleum Corporation for three periods of 15, 23 and 29 days.

Table 2 lists the available information on the amplitude and epoch of the semidiurnal tide. Data for positions between Las Piedras and Maracaibo represent long term averages supplied by Servicios Hidrograficos, formerly the Maracaibo Bay Survey. For Aruba and La Salina the characteristics listed are those of the M_2 constituent as found by harmonic analysis. The data for Bobures, near the head of the lake, was supplied by Creole Petroleum Corporation. Tidal observations in the lake are difficult because of the small range of tide, rapid changes in lake level and the frequent occurrence of seiches which obscure the tidal record. The Bobures data are based on an average of 6 successive days of record selected for a period when seiches were absent. Additional information supplied by the Compãnia Shell de Venezuela

TABLE 2. *Data on semidiurnal tide*

Position	Latitude (N.)	Amplitude (cm)	High Water* (hr)	Slack Water* Turns South (hr)
Aruba	12°31′	4	−3.5	
Las Piedras	11°42′	12.5	−0.5	
Zaparita	11°01′	46.0	0	−3.6
Zapara I	10°58′	32.4	+0.8	−3.2
Tablazo Bay				
Buoy T-5	10°56′			−2.8
Buoy T-11	10°54′	25.0	+1.1	−1.1
Buoy T-17	10°52′			+0.6
Buoy T-23	10°50′			+1.4
Punta de Palmas	10°47′	24.6		+1.8
Capitan Chico	10°43′			+0.5
Maracaibo	10°38′	10.7	+1.2	
Puerto Escondido	10°30′			+0.8
La Salina	10°23′	0.7	+1.4	−0.5
Bobures	9°15′	3.0	+6.0	−1.0

* Time relative to high water at Zaparita.

indicates that at five other positions on the southern margin of the lake, extending from La Iguana (10°02′N, 71°60′W) to La Ceiba (9°28′N, 71°14′W), the range and time of high water were similar to that observed at Bobures.

The current data listed in Table 2 were obtained by field observations, using current poles and drags (Pritchard and Burt 1951), extending usually over not more than one day. Because of the variations in amplitude which occur in the course of the lunar cycle, and the considerable and variable outflow of fresh water from the lake, these data give only rough approximations of the mean tidal motion.

THE SEMIDIURNAL TIDE

Two independent methods of analysis have been employed. The first depends on the characteristic phase relations of elevation and current in a standing oscillation. The second employs step-by-step integration of finite difference equations for continuity and acceleration under the force of gravity.

Location of node and antinode by phase relations

If the tide in an embayment is considered to be a standing wave resulting from the combined effects of a primary wave entering from the outer sea and a secondary wave resulting from the reflection of the preceding entering wave at the barrier formed by the head of the embayment, these waves will be in phase to a different degree at different positions along the channel. Nodes will exist where the two waves have opposite phases at distances of ¼, ¾, etc., wave lengths from the barrier. Antinodes will exist, where the two waves have the same phase at ½, 1, etc., wave lengths from the barrier. Equations expressing the relation of the times of high water, slack water, elevation, current along the channel, and the effect of friction on these relations are available (Redfield 1958). For present purposes it will serve to summarize the conditions found at the barrier and at the first node and antinode. If friction is neglected:

1) At the barrier high water and slack water are synchronous, the amplitude of elevation is maximal and that of current is zero.

2) At the node the amplitude of elevation is zero, that of current is maximal and the time of high water changes abruptly by ½ period, with the result that the elevation is rising beyond the node while it is falling between the node and the barrier.

3) At the antinode the amplitude of elevation is again maximal and that of the current is zero. The time of slack water changes abruptly by ½ period with the result that high water and slack water become synchronous beyond the antinode and occur ½ period before high water at the barrier.

If friction is taken into account the changes in phase at the node and antinode are less abrupt. The amplitude of elevation at the node and of current at the antinode are not reduced to zero but remain minimal, and while the change in phase is less abrupt, these points are still marked by a maximal rate of change of the time of high and slack water. These relations are shown in Figure 5.

Current measurements made off Captain Chico showed that in the Strait of Maracaibo the tidal current flowed seaward during the period when the tide was rising. This is the relation expected between a node and

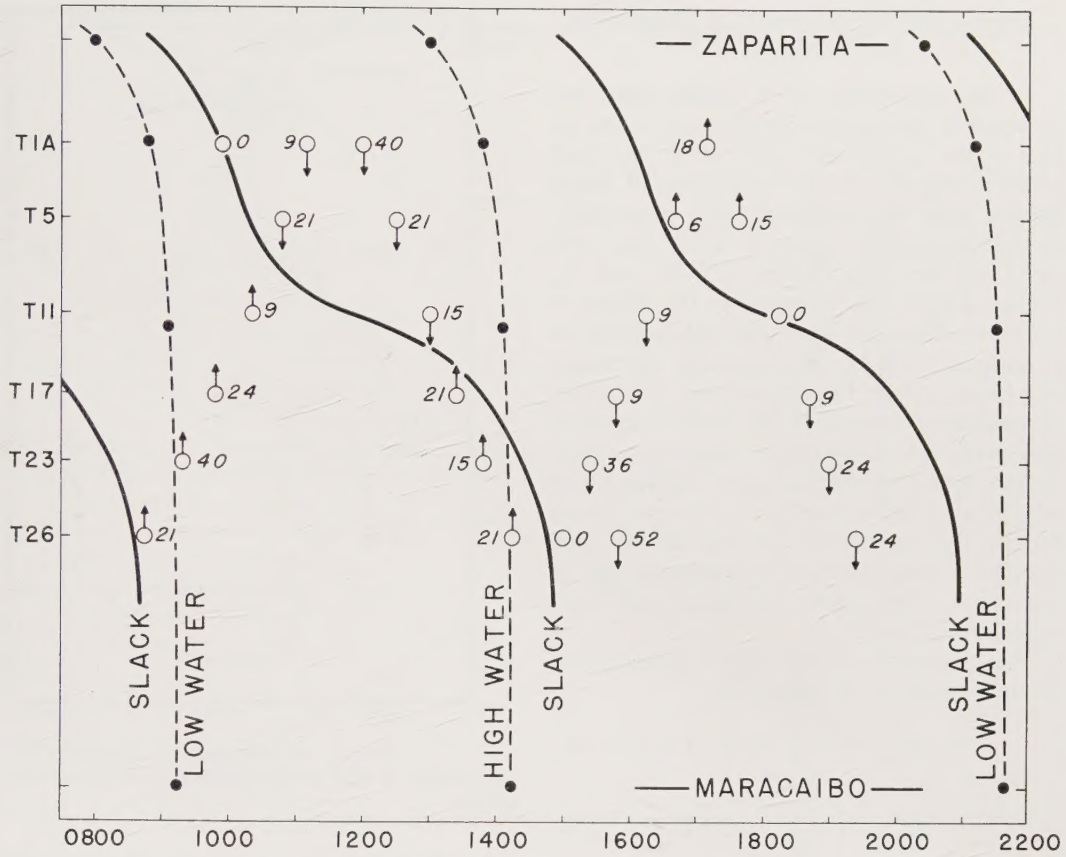

FIG. 2. Relation of time of high water and slack water in Tablazo Bay. March 15, 1954 Time meridian 67°30'W. Current velocities in cm/sec.

antinode (see Fig. 5). Since the current flows landward while the tide is rising in the passage leading from the Gulf of Venezuela it was suspected that an antinode existed in Tablazo Bay. The position of this antinode was determined by the following expedient.

Four traverses of the channel between Punta de Palmas (Buoy T-26) and Zapara Island (Buoy T-1A) were made in alternate directions. At 6 positions marked by navigation buoys the direction and velocity of current were measured in passing. The measurements are plotted in Figure 2 against the time of observation. The continuous curves show the time of slack water with very little uncertainty. The dashed lines indicate the predicted time of high water. The figure shows that the direction of flow is opposite at all times at Zaparita and Punta de Palmas, and that the time of slack water changes rapidly through ½ period in the neighborhood of Buoy T-11 at about 10°54'N. Since these are the relations expected in the neighborhood of an antinode it is concluded that the antinode of the semidiurnal tidal components exists near this point.

The position of the node of the semidiurnal tide cannot be located precisely from the available data on the times of high and slack water. They indicate that the node must lie in the lake at a point south of La Salina, since high water is delayed at La Salina only 0.3 hr relative to its time at the antinode. La Salina must lie close to the node, however, since the amplitude of the semidiurnal tide is greatly reduced there.

Analysis by Consideration of Continuity and Acceleration

If the dimensions of an embayment are accurately known the distribution along its axis of the amplitude of elevation, flux and current velocity for an oscillation of given period may be estimated. The procedure, first developed by Sterneck (1915) has been used by him, by Defant (1919) and by Grace (1936) in examining the tides in various landlocked seas, and is described by Proudman (1953). It consists in determining from a chart the dimensions of a series of segments separated by vertical sections across the axis of the basin. Begining at high or low water at the landward segment, the amplitude of elevation in each segment and of the flux and mean current across each section is obtained by the alternate use of two finite difference equations and successive integration.

For frictionless flow the approximate finite difference equations are:

$$\delta (AU) = \left(\frac{2\pi}{T} \cdot b \cdot \delta x \right) Z \qquad (1)$$

$$\delta Z = -\left(\frac{2\pi}{gT} \cdot \delta x \right) U \qquad (2)$$

where A = area of each vertical section
U = amplitude of mean current across section
b = breadth at section
δx = distance between sections
Z = amplitude of elevation of each section
g = acceleration due to gravity
T = period of tidal component

If friction is considered, equation (1) is replaced by

$$\delta (AU_1) = \left(\frac{2\pi}{T} \cdot b \cdot \delta x \right) Z_1 \qquad \text{and}$$

$$\delta (AU_2) = \left(\frac{2\pi}{T} \cdot b \cdot \delta x \right) Z_2 \qquad (3)$$

and equation (2) by

$$\delta Z_1 = \left(-\frac{1}{gT} U_1 + \frac{1}{g\tau} U_2 \right) 2\pi\delta x \qquad \text{and}$$

$$\delta Z_2 = \left(-\frac{1}{gT} U_2 - \frac{1}{g\tau} U_1 \right) 2\pi\delta x \qquad (4)$$

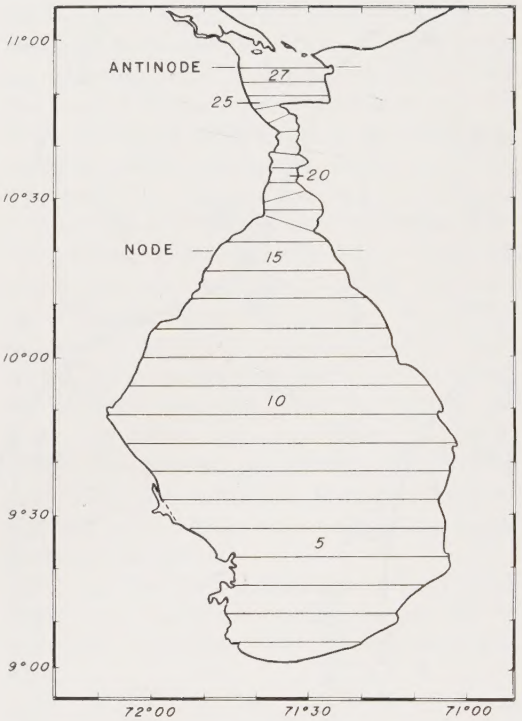

FIG. 3. Scheme of segmentation employed in calculation of tidal characteristics by stepwise integration.

At each section the amplitude of the mean current $= \sqrt{U_1^2 + U_2^2}$ and the amplitude of elevation $= \sqrt{Z_1^2 + Z_2^2}$. The characteristic damping time constant, τ, is given by $\frac{2\pi}{\tau} = \frac{\delta k}{3\pi h} C$ where k is the coefficient of friction, h is the mean depth, and $C = \sqrt{U_1^2 + U_2^2}$.

The distribution of amplitude of elevation, of flux and of mean current along the axis of the Maracaibo system was estimated by dividing the area into 27 segments, as shown in Figure 3. The spacing of the sections, δx, was 10 km in the lake and about 5 km along the strait and across Tablazo Bay. The dimensions of the sections and of the surface areas between sections were obtained from a large-scale chart, contoured at 1-m depth intervals, provided by the Creole Petroleum Corporation.

The results of application of equations (1) and (2) for frictionless flow are shown in Figure 4 by solid lines. They indicate the

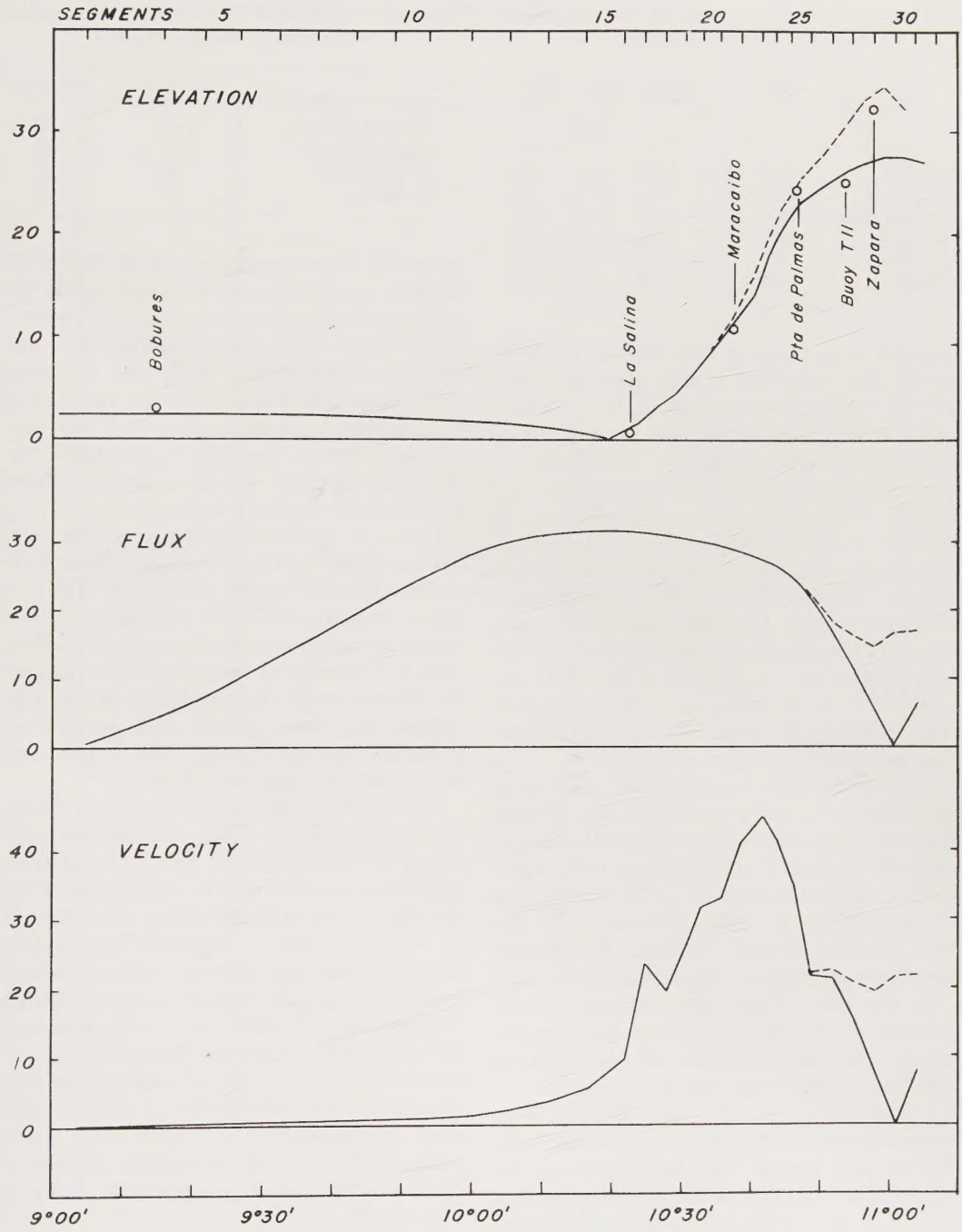

FIG. 4. Amplitude of elevation, flux and mean velocity of current estimated by stepwise integration. Solid lines show estimates for frictionless flow; dashed lines assuming coeffficient of friction, $k = 0.0025$. Scale of ordinate: elevation, cm; flux, 10^4 cm^3/sec; mean velocity, cm/sec. Abscissa—latitude N. and position of segments.

TABLE 3. *Comparison of observed and calculated amplitude of semidiurnal tide (cm)*

Position	Observed	Calculated ($k = 0$)	Difference	Calculated ($k = 0.0025$)	Difference
Zapara I	32.4	29.0	−3.4	33.0	+0.6
Buoy T-11	25.0	26.4	+1.4	30.5	+5.5
Punta de Palmas	24.6	22.0	−2.7	24.0	−0.6
Maracaibo	10.7	12.5	+1.8	12.0	+1.3
La Salina	0.7	0.75	+0.05	1.0	+0.3
Bobures	3.0	2.5	−0.5	2.5	−0.5

location of a node in the lake at 10°20′N where the elevation passes through zero, and where the flux is maximal. If the calculation is extended to include several hypothetical segments, similar in dimensions to segment 27, current velocity and flux are found to pass through zero in segment 29 indicating that an antinode would exist in that region if Tablazo Bay were somewhat longer. The available data for the amplitude of elevation may be fitted best by the estimates if the amplitude at the head of the lake is taken as 2.5 cm. See Table 3. If the value of 3 cm observed at Bobures is used the amplitudes at Maracaibo and in Tablazo Bay become too large.

The calculation was repeated employing equations (3) and (4) which take bottom friction into account. The value of the coefficient of friction, k, was taken as 0.0025 following the estimations of Taylor (1918) and Grace (1936) for tidal movement in the Irish Sea and Bristol Channel. The results are shown in Figure 3 by dashed lines.

In the lake, where the estimated mean velocity of the tidal current is less than 10 cm/sec, the friction terms are insignificant and flow may be regarded as frictionless. In the strait of Maracaibo and Tablazo Bay, where the estimated velocities of the tidal current are higher, the friction terms increase the estimates of the amplitudes, flux and current. The estimated amplitudes agree with the available observations shown in Table 3 about as well as they do in the frictionless case. The position of the node is unchanged. Current velocity and flux do not fall to zero in the apparent position of the antinode, but pass through minima between the hypothetical segments 28 and 29. Such a condition is to be expected at the antinode in the presence of friction because the reflected tidal wave is attenuated and complete interference with the incoming wave does not occur, with the result that some residual current is present. It also corresponds to the observation that tidal currents are present at all positions across Tablazo Bay as shown in Figure 2.

TABLE 4. *Comparison of observed and calculated amplitude of current (cm/sec)*

	Observed	Calculated
Punta de Palmas	30	32
Capitan Chico	30	42
Pt. Esundido	16	25
La Salina	12	12

Data are not available for a precise comparison of the currents, but a few short-term current measurements shown in Table 4 agree roughly with the estimations. The observed currents may be expected to differ from the estimated mean currents because of differences in the amplitude of the tide during the lunar month and because of variations in the current with depth and with position across the channel.

The stepwise integration indicates clearly the position of the node, and the insignificance of friction in the lake. It estimates approximately the relative amplitudes of the elevations and currents along the channel. It does not yield completely satisfactory estimates since the solutions with or without friction do not develop the antinode within Tablazo Bay. Nevertheless, when it is considered that the stepwise integration is carried out over a half wave length of the tide, in a channel which varies 15 fold in both depth and breadth the effectiveness of the method in estimating the general characteristics of the tide in an irregular basin is impressive.

Discussion of the semidiurnal system

The relations of the times of high water and slack water, and the approximate results of the stepwise integration justify the conclusion that the tide of the Maracaibo Sys-

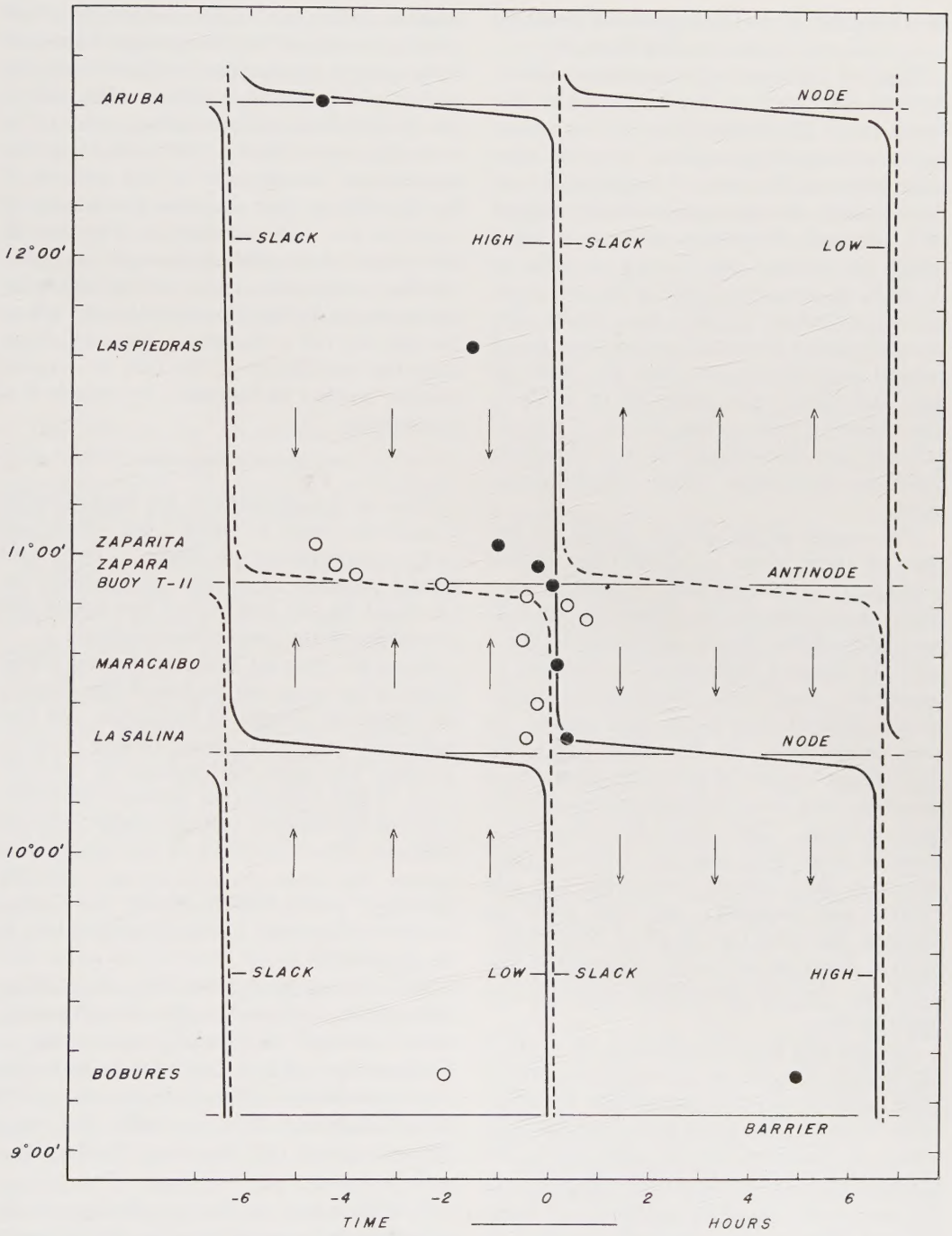

FIG. 5. Diagram of theoretical relations of times of high and low water (solid lines), slack water (dashed lines) and current direction (arrows) for a standing wave reflected from a barrier. Solid circles show data for time of high water, and open circles for time of slack water as listed in Table 2. Ordinate, time in hours relative to high water at Buoy T-11; abscissa, latitude N.

tem behaves as a standing wave resulting from reflection at the head of the lake.

Figure 5 attempts to present the available data on tide and current in relation to this conclusion. The heavy lines in this figure represent in a diagrammatic way the relations between the time of high water and slack water to be expected on this hypothesis in a channel of uniform section ¾ wave length in extent, and having a node at 10°20′N, an antinode at 10°54′N, and a second node at about 12°30′N, near Aruba. The arrows indicate the synchronous direction of current and the points show the times of high and slack water recorded in Table 2. The observed data corresponds in a general way to the theoretical curves. However, there are departures which require comment.

The scatter of the points indicating the time of slack water is attributable to the inadequacy of current data obtained from a single day's observation where the diurnal inequality of the tides is pronounced. Similarly the time of high water at Bobures is based on short term observations made under difficult conditions and cannot be very dependable. On the other hand, the times of high water at the other positions is based on long term averages and should be quite reliable. They show that there is a delay of more than one hour between high water in the Gulf of Venezuela (at Las Piedras and Zaparita) and high water in Tablazo Bay and the Strait of Maracaibo. Such a delay is not to be expected if the tides are due to the simple cooscillation postulated.

Tablazo Bay is separated from the Gulf of Venezuela by narrow passages in which swift currents develop in response to differences in level. The delay in the time of high water in Tablazo Bay is adequately explained by the restriction of these passages. Because of the break in continuity of unrestricted flow in the channels leading to Tablazo Bay it is probably mistaken to consider the Gulf of Venezuela and Lake Maracaibo as forming a simple system of oscillation.

It is perhaps more correct to consider the motion of the lake to be a uninodal seiche which, because of the dimensions of the lake basin and its approaches, oscillates with the period of the semidiurnal tide. The tide in the Gulf of Venezuela, which appears to be a simple cooscillation dominated by the semidiurnal constituents of the motion in the Caribbean Sea, provides the energy to maintain the lake's oscillation. The flow in the restricted connecting passages is similar to that commonly observed in inlets to embayments behind barrier islands, where the rise and fall of the tide is delayed. Similarly the oscillation of the lake is delayed relative to that in the Gulf, by which it is engendered.

THE DIURNAL TIDE

Data on the diurnal tide are limited to the 5 positions, listed in Table 1, for which harmonic analyses are available. These data should conform to certain expectations determined by the position of the nodes and antinodes of the semidiurnal system.

Since the diurnal and semidiurnal waves travel at the same rate and the former waves are twice the length of the latter, the first node of the diurnal system should occur in Tablazo Bay, near the position of the antinode of the semidiurnal system. The antinode of the diurnal system should coincide with the second antinode of the semidiurnal system, but since no such second antinode develops within the limits of the coastal waters no antinode for the diurnal tide is to be expected.

Considering the epochs of the diurnal constituents, the value of G should be about the same seaward of the expected node in Tablazo Bay, which may be seen to be the case. Landward of the node the value of G should increase 180°. Actually the value changes about 135° between Tablazo Bay and La Salina.

Consideration of the amplitudes of the constituents is complicated by the influence of the dimensions of the basin. It may be noticed that between Aruba and Zaparita the amplitudes of the diurnal constituents are not greatly augmented as is that of the M_2 constituent, for which the dimensions of

the Gulf produce a high degree of resonance. Between Zaparita and Tablazo Bay both species of constituent diminish about in proportion, presumably as the result of changes in the dimensions of the channel. At La Salina the amplitude of M_2 is reduced much more than that of the diurnal constituents because this position is close to the node of the semidiurnal system.

It may be concluded that the diurnal constituents conform reasonably, if not exactly, to the characteristics of the system deduced for the semidiurnal tide.

DISCUSSION

The tide in the Maracaibo system has been treated as linear motion parallel to the axis of the basin. The existence of a significant rotatory system is excluded by the following consideration.

It may be inferred from the existence of the node for the semidiurnal tide near the northern extremity of the lake that the natural period of lengthwise oscillation of the lake proper is about 6 hr. Since the width of the lake is about ⅔ of the length a transverse oscillation would have a period of perhaps 4 hr. A rotatory system requires the components of motion at right angles to be comparable in period. Consequently such a system could not exist for a tide of 12-hr period.

In the Northern Hemisphere the rotation of the earth frequently causes the range of tide in an embayment to be greater on the right of the inflowing current—the Kelvin effect. Such effects in Lake Maracaibo appear to be insignificant because of the low current velocities and the low latitude. Taking the mean velocity of the tidal current at the widest part of the lake to be 0.5 cm per sec and applying the geostrophic equation, it appears that if equilibrium between the Coriolis force and gravity were reached the transverse slope of the lake surface would be about 10^{-8} and the difference in elevation on opposite sides would be less than 2 mm. A similar computation for the Strait of Maracaibo at Capitan Chico, where tidal currents of 30 cm/sec occur, indicates a slope of less than 10^{-6} and a difference of elevation of less than 5 mm.[2]

The presence of the antinode in Tablazo Bay appears to have an important bearing on the problem of maintaining the channel, and, in fact, on the development of the physiography of the area. The topography suggests that in comparatively recent times Lake Maracaibo stood above sea level. The form of the strait resembles a river valley eroded under arid conditions, and a deeper trough along its western side indicates the course of the river which once drained the lake. The postglacial rise in sea level appears to have drowned this valley and to have given access of tidal water to the lake. Subsequently marine deposits filled the bight in which Tablazo Bay lies and built the barrier islands and bars which separate it from the Gulf of Venezuela (Redfield 1958).

With the admission of the tide into the lake the antinode would have developed. Since an antinode is a region where flux and current are greatly reduced, sedimentation would be encouraged there. When sea level was lower and the water shallower the antinode may have been located south of its present position. It is possible that a sill at the southern end of the strait, which separates the deeper waters of the strait from those of the lake basin and where the remnants of the old river course appear to have been buried, may have been deposited when the antinode occupied this position. However that may have been, at the present time the antinode is in a position to account for the deposition of the marine sediments which fill Tablazo Bay. In 1954 the ship channel across Tablazo Bay had shoaled in just the region where the antinode was located, and dredges were at work there removing the recent sedimentation.

The antinode appears to be important also in restraining the entrance of salt water into the lake. The low chloride content of lake

[2] Within Lake Maracaibo currents, presumably wind-driven, circulate in an anticlockwise sense with velocities of the order of 25 cm/sec (Redfield 1958). The tidal currents under discussion are superimposed upon this motion and the discussion refers only to the tidal component of motion.

water, which has varied between 400 and 1,200 ppm during the past 14 years, is due to the large discharge of lake water required to balance the precipitation over the lake basin. During rainy periods this discharge is sufficient to displace the water of Tablazo Bay almost completely—a possibility arising from its very shallowness and which, in turn, may be attributed to sedimentation at the antinode. During dry periods this flow diminishes and salt moves inward across Tablazo Bay and into the lake by tidal mixing. The reduction of tidal flux in the region of the antinode limits this process and thus reduces at such times the rate at which salt penetrates to the lake waters.

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SOURCES OF PHOSPHORUS AND NITROGEN FOR LAKES ON AFOGNAK ISLAND[1]

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ABSTRACT

The contribution of inlet streams to the phosphorus and nitrogen budgets of two lakes on Afognak Island (Kodiak Region), Alaska has been studied with special reference to the morphology of the associated watersheds. One lake drains a steep, vast watershed; the other, a relatively flat, restricted one. Streams coming from the steeper slopes show a lower PO_4-P concentration than those coming from shallow slopes as might be expected from runoff–residence considerations. Exactly the opposite is found when the nitrate concentration of these streams is examined, *i.e.*, only the streams arising on steep slopes show appreciable amounts of nitrate. Phosphorus appearing in the inlets probably originates in the Katmai ash which lies just under the humus layer of soil. Three distinct layers of ash occur normally. A complex pattern of phosphorus distribution can probably be attributed to differences in the permeability of these layers to water. A model has been constructed as an aid to interpretation of the data. Thickets of nitrogen fixing alders, found only along steep stream banks, may be the source of the nitrate content of these streams.

INTRODUCTION

Interest in the exogenous sources of phosphorus and nitrogen for the lakes of southwestern Alaska has originated in the problem of production of young red salmon (*Oncorhyncus nerka*). Juday, *et al.* (1932), Barnaby (1944), Nelson and Edmondson (1955), Eicher and Rounsefell (1957), and Rounsefell (1958) have discussed various relationships between these important elements and the productivity of lakes in that area. In 1956, we began an investigation into the gains and losses of these elements from several lakes near Kitoi Bay, Afognak Island, Alaska. Eventually we hope to acquire sufficient information to allow calculation of relatively accurate phosphorus and nitrogen budgets. The results reported here were obtained during the summer of 1958 and are concerned primarily with a study of the effect of watershed morphology upon the concentrations of these elements in the inlet streams of the lakes.

Afognak Island lies just north of Kodiak Island; a few miles of open water serve to separate the two. Kitoi Bay lies near the eastern end of Afognak Island, 30 air miles north of the city of Kodiak. The Japan Current here produces a uniformly cool and damp climate. Precipitation is well distributed throughout the year and averages 60.6 in. annually. There are, on the average, 163 days each year with at least .01 in. of precipitation and many of the remaining days are overcast. The maximum monthly mean temperature, 54.3°F, occurs in August and the minimum, 29.5°F, in January. These statistics apply to Kodiak where weather records have been kept for about 50 years. A reporting station is now maintained at Kitoi Bay and it appears that the climate there is very much the same as that of Kodiak.

Numerous lakes occur over the surface of the island. The majority lie along fault lines scoured by glaciers and in piles of morainal rubble. These lakes collect drainage from small watersheds with low mean slope and tend to show a yellow or brown color when viewed from the air. Fjord and piedmont lakes also occur, usually close to tidewater. These collect water from comparatively vast

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TABLE 1. *Pertinent morphological features associated with Little Kitoi and Upper Jennifer Lakes*

	Surface area (ha)	Watershed area (ha)	Turnover, years	Mean depth, (m)	Max. depth, (m)	Index of shoreline irregularity
Little Kitoi Lake	42.0	731	0.35	9–10 (estimated)	28	1.8
Upper Jennifer Lake	44.3	94	2.20	10.4	29	2.5

watersheds consisting of many steep slopes and do not give the impression of yellow color.

Over most of the island the watersheds and lake bottoms are covered with layers of volcanic ash laid down by the eruption of Mount Katmai in 1912. A single analysis made in 1918 (Griggs 1920) of ash collected from Kodiak Island showed a phosphorus content of about 3200 ppm (as P_2O_5) pointing to the possibility that the Katmai ash could have been a prime source of large quantities of that element. The same possibility is suggested by tree-ring studies at Kodiak (Griggs 1920), Kitoi Bay (ADF 1955), and Brooks Lake (Eicher and Rounsefell 1957) showing increased growth after the ashfall, and also by descriptions of the lush vegetation on the northern part of Kodiak Island several years after the eruption. The nitrogen content of the ash was low, amounting to about 8 ppm (Shipley 1920a) and it is therefore unlikely that the ash was an important source of that element.

Our working hypothesis has been based upon the assumption that if the phosphorus originally contained in the ash was leachable, differences in the extent of leaching would now be correlated with the average slope of the watershed. We expected to find more phosphorus remaining in ash lying on a steep watershed than on a less steep one inasmuch as on the former, precipitation would have tended to run off the surface more quickly with little penetration and leaching of the ash itself. Our research program consisted of: 1) obtaining water samples from inlet streams and vertical series of water samples from the associated lakes with subsequent analysis for phosphorus and nitrogen, and 2) obtaining core samples from the associated watersheds and analyzing them for phosphorus content.

Little Kitoi and Upper Jennifer lakes were selected for study. A summary of certain general morphometric and physical characteristics of the two lakes will be found in Table 1. They are essentially alike in these respects with two important exceptions: 1) size of watershed, Little Kitoi draining an area roughly seven times that drained by Upper Jennifer, and 2) index of shoreline irregularity, the index for Upper Jennifer Lake exceeding that for Little Kitoi Lake by a considerable amount, a fact correlated with the probable origins of the two lakes. Upper Jennifer appears to be the result of glacial scouring, apparently lying in morainal rubble. Little Kitoi Lake occupies a cryptodepression, the deepest point lying about 20 m below mean sea level. (At high water during spring tides, the lake surface is often only about 2 m above salt water. There are no indications, however, of actual salt water invasions of the lake.) A rock bar which forms the south shore serves to separate the lake from the ocean. Little Kitoi Lake is therefore a fjord lake, occupying a valley overdeepened and dammed by a glacier. The lakes and their associated watersheds are shown diagrammatically in Figure 1. Details of the temperature and oxygen cycles, light transmission, and certain other characteristics of these lakes will be published elsewhere. For the present it will be sufficient to mention that they are dimictic lakes of the second thermal class (Hutchinson 1957) and that the oxygen curves, although of quite divergent shapes, indicate an oligotrophic status for both.

METHODS

Phosphorus in lake and stream waters

A stannous chloride-reduced molybdophosphoric blue color method, outlined by

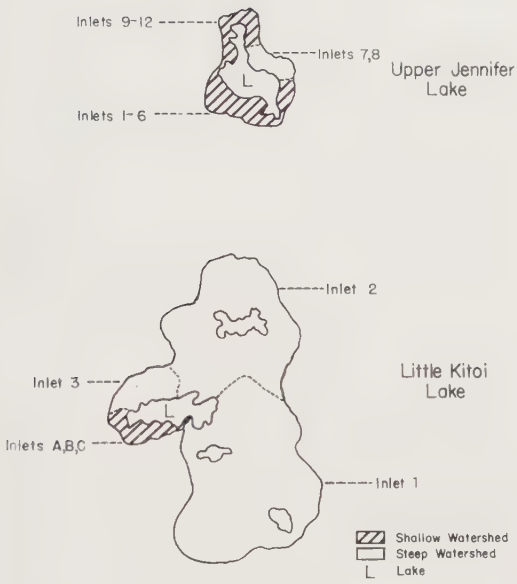

FIG. 1. Maps of the study lakes and their associated watersheds.

Jackson (1958), was selected for the phosphorus determination; it has the highest sensitivity of the stannous chloride-reduced procedures. With 5-cm cells read in a Beckman Model B spectrophotometer, concentrations down to about 5 μg/L PO_4-P could be determined. Total phosphorus concentrations often approached or reached this value; however, soluble PO_4-P seldom exceeded 2 μg/L and often fell below 1 μg/L. It was therefore necessary to concentrate the samples and this was accomplished by boiling. The latter procedure, however, often produced a yellow color which showed significant absorption at the wavelength used (660mμ); the sample was therefore read after the addition of all reagents except stannous chloride and again after addition of the reducing agent, thus eliminating the effect of the yellow color.

Particulate material was excluded from samples used for determination of soluble fractions by millipore filtering within one or two hours after collection. Oxidation of organic fractions was performed with perchloric acid digestion according to Robinson (1941). A loss of total phosphorus was sometimes experienced with samples requiring an unusually long digestion.

Nitrate in lake and stream waters

The method of Mullin and Riley (1955) in which nitrate is reduced to nitrite and a pink color subsequently developed with 1-naphthylamine hydrochloride was used with a boric acid buffer (made possible since we were using only fresh water samples). The buffer modification reduced the scatter of standard points and resulted in an even more satisfactory method. Samples were read in a Beckman Model B spectrophotometer in 1-cm cells.

Phosphorus in soil and ash

A 1.0 N acid-ammonium fluoride extraction procedure (Jackson 1958, p. 162) followed by a stannous chloride-reduced molybdophosphoric blue color in hydrochloric acid (Method II of Jackson 1958) was used. Absorbances were read in a Beckman Model B spectrophotometer in 1-cm cells. The range of the method was entirely satisfactory for the phosphorus levels encountered. Calcium phosphate, aluminum phosphate, and some of the iron phosphates are included with this extraction. Concentrations in duplicate soil samples agree with 1 or 2 digits in the third decimal place.

The possibility that arsenic might be present and erroneously reported as phosphate has been eliminated by determining the total phosphorus content of several ash samples. Perchloric acid digestion was followed by phosphorus determination with Method IV of Jackson (1958) in which provision is made for arsenic elimination through reduction with bisulfite. No differences were detectable between samples treated with bisulfite and those which were not. Total phosphorus determinations made in this way yielded results about 20% higher than those obtained by the acid-fluoride extraction procedure.

RESULTS

Phosphorus in lake and stream waters

The inlet streams supplying Upper Jennifer were located first by examining stereo pairs of aerial photos. Twelve were discovered and their existence confirmed by cruis-

TABLE 2. *Concentrations of various phosphorus fractions and of nitrate in the inlet streams, July 25–26, 1958*

	Inlet	Slope	PO_4-P (μg/L)	Soluble organic P (μg/L)	Total P (μg/L)	NO_3-N (μg/L)
Little Kitoi Lake, July 25, 1958	A	.15	0.94	3.2	6.1	10
	1	.17	0.69	3.0	6.2	5
	2	.28	0.69	2.1	2.8	25
	3	.26	0.66	2.4	2.4	53
Upper Jennifer Lake, July 26, 1958	10	.09	2.25	1.2	3.9	5
	4	.10	1.44	3.7	6.1	8
	9	.12	0.94	3.1	4.8	7
	5	.14	1.00	4.4	—	5
	8	.29	0.56	3.3	—	27
	7	.39	0.44	3.4	—	15

ing the shoreline. No additional streams were revealed in the cruising. The inlet streams to Little Kitoi were known from previous experience on this lake. The locations of the streams can be seen by reference to Figure 1. In general the inlet streams to Upper Jennifer can be characterized as short, coming from shallow slopes, and having small volumes of flow. Inlets 7 and 8, however, come from the single steep hill; striking differences between these and the others are shown below.

The inlet streams supplying Little Kitoi are somewhat more complex in that streams 1 and 2 drain relatively vast areas through small intermediate lakes. Inlets A, B, and C drain small, relatively level, sphagnum-covered watersheds and are therefore comparable to most of the Upper Jennifer inlets. Average slopes for all inlet streams have been calculated from topographic maps simply by measuring the horizontal length of the stream and the vertical rise. Inlet streams 1 and 2 of Little Kitoi caused some complications and the slopes in subsequent tables are rather crude, representing the average of several arbitrarily selected tributaries. As would be expected, the volumes of flow in Little Kitoi inlet streams 1, 2, and 3 far exceed the flow in any of the Upper Jennifer inlet streams. Several sets of determinations of soluble PO_4-P, soluble organic P, and total P were made on samples from inlet streams in the course of the summer. Although the absolute concentrations varied from one sampling to another, the relative values among the streams remained practically constant. The phosphorus analyses carried out on water from selected inlet streams of both lakes, collected on July 25 and 26, are presented in Table 2 along with the slopes of the various streams and the results of nitrate determinations. The postulated inverse relationship between watershed slope and phosphorus content of the stream is substantiated by these data, particularly when a closer examination is made of the PO_4-P fraction, which is plotted against stream slope in Figure 2. The points from Upper Jennifer streams lie on an hyperboloid curve. The inlet streams to Little Kitoi do not range so widely in slope, but cluster about the curve rather well, with values for inlets A and 2 falling exactly on the curve. The latter two inlets drain watersheds having essentially the same vegetation as those of Upper Jennifer, a ground covering of sphagnum with stands of Sitka spruce (*Picea sitchensis*). The areas to the west of Little Kitoi drained by inlets 2 and 3 have a dense cover of fern in some places.

Analyses of stream water available for Little Kitoi on July 8, and for Upper Jennifer on July 10, can be used to calculate PO_4-P retention rather crudely by making the following assumptions: 1) that all precipitation falling upon a given watershed during the month of July eventually appeared in the lake and that subsequently an equal amount left through the outlet, 2) that all this precipitation appeared at the mouths of the inlet streams with a phosphorus concentra-

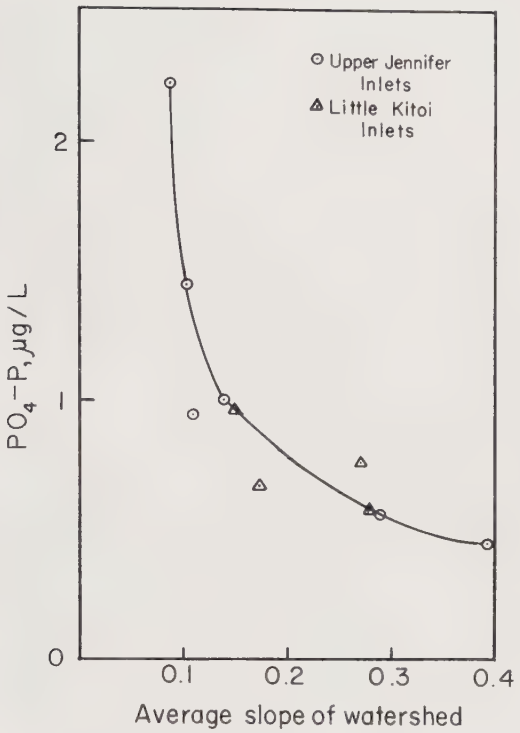

FIG. 2. Relationship between average slope of a watershed, and the PO_4-P concentration of the associated inlet stream, July 25–26, 1958.

tion equal to that measured on a single date in July and that the concentration of phosphorus in the outlet water did not vary from that measured on the same date in July, 3) that a valid mean concentration of phosphorus can be calculated by taking the simple average of inlet determinations for a single lake, and 4) that no evaporation takes place.

On July 8 the mean inlet stream PO_4-P concentration amounted to 1.05 µg/L, while the outlet stream PO_4-P concentration equaled 0.95 µg/L. Combining these values with the precipitation for July (22.1 cm), making an allowance for the rain falling directly on the lake and making the assumption that this rain contained no phosphorus as PO_4, we have calculated a net retention of 80 kg PO_4-P for Little Kitoi Lake during the month of July. Dividing by the volume of the lake, this increase amounts to .019 µg/L, about 2% of that already present in the same form and, analytically, an undetectable amount.

On July 10, the mean PO_4-P content of Upper Jennifer inlets was 1.69 µg/L; the outlet concentration was 0.85 µg/L. The same procedure outlined above yields a value of 93 kg for the PO_4-P retained by this lake during July, or .020 µg/L of lake water. With these crude calculations we can only say that no difference between the two lakes in the absolute rate of PO_4-P retention is detectable.

Two vertical series from each lake were analyzed for the same phosphorus fractions mentioned above. Those of July 8 and July 10 are presented in Table 3. There appears to be no obvious vertical stratification of any particular fraction in either lake, nor do there seem to be any striking differences in any of the mean concentrations.

Nitrate in lake and stream waters

The nitrate contents of the various inlet streams show direct correlation with their slopes. In both lakes the steeper watersheds are found to give rise to streams with considerably higher NO_3-N concentrations than those from the less steep watersheds (Table 2). The total amount of nitrate entering Little Kitoi is, however, considerably greater than that entering Upper Jennifer.

One possible explanation for the correlation between slope and nitrate content of these streams lies in the ability of alder (*Alnus* sp.) to fix molecular nitrogen. In various glaciated regions of Alaska there is a serious deficiency of combined nitrogen in the soil immediately following glacial retreat; this deficiency seems to be made up upon appearance of alder. The ability of alder to fix nitrogen has been demonstrated experimentally; the activity apparently resides in root-nodules. A description of the role of alder as a nitrogen fixer is given by Lawrence (1958). He and his co-workers found that young alder thickets in southeast Alaska, 5 years old and 5 ft high, added 158 kg/ha of nitrogen to the soil each autumn through their fallen leaves. Alder thickets on Afognak Island grow profusely only on steep slopes adjacent to swift streams. If

TABLE 3. *The vertical distribution of phosphorus fractions in Little Kitoi Lake (LK), July 8,1958 and in Upper Jennifer Lake (UJ), July 10, 1958*

Depth in meters	0	3	5	6	10	15	20	21	Mean concentration
				PO_4-P, μg/L					
LK	0.9	1.2	—	1.1	0.8	0.9	—	0.8	1.0
UJ	0.7	0.8	0.9	—	0.9	0.5	0.6	—	0.8
				Soluble organic P, μg/L					
LK	2.0	2.6	—	2.0	2.8	3.4	—	2.1	2.5
UJ	1.8	1.4	1.6	—	1.0	1.9	1.2	—	1.5
				Total P, μg/L					
LK	4.6	9.8	—	4.2	3.8	3.6	—	5.6	5.3
UJ	4.4	—	4.0	—	5.0	4.6	5.9	—	4.8

they behave in the same manner as those studied by Lawrence, it seems entirely possible that they may be the source of the nitrate in these streams.

The nitrate contents of both lakes was followed during the summer. Their vertical distribution of nitrate on July 7, 1958 is shown in Figure 3. In the upper 5 m of Little Kitoi the nitrate concentration was very low, never higher than 10 μg/L. From 5 to 10 m there was a sharp rise to almost 40 μg/L and from there a slower increase to the bottom. Such a distribution was probably the result of nitrate uptake by organisms in the euphotic zone. The entire lake should be expected to exhibit a nitrate distribution uniform from top to bottom following spring circulation, with the nitrate content approximately equal to that of the hypolimnion later in the season. Between June 30 and July 7, however, the concentration within the hypolimnion of Little Kitoi increased by nearly 50%. Since, at this time, the oxygen concentration at the deepest point in the lake was still high, an exogenous source of nitrate is indicated. Temperatures of the inlet streams ranged from about 6°C to 12°C and with the relatively large volumes of flow involved, it seems possible that incoming water may drop well below the surface, carrying nitrate into the hypolimnion.

In Upper Jennifer Lake, however, nitrate was almost undetectable in the upper 10 m, and from there it very gradually increased to a maximum of about 20 μg/L at the bottom. This pattern persisted during the entire summer. The nitrate was thus largely used up except in the deepest water, and the concentration there indicates that even during the vernal circulation, only relatively small amounts of nitrate were present. No increase in nitrate was observed in the hypolimnion during the summer.

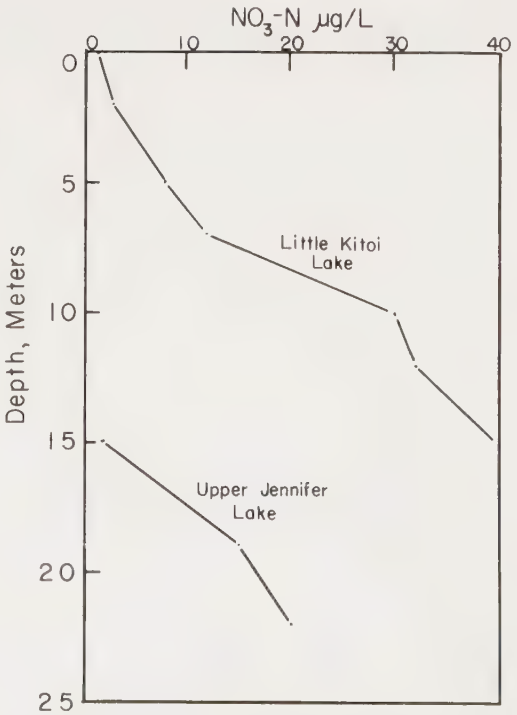

FIG. 3. The vertical distribution of nitrate in Little Kitoi and Upper Jennifer lakes on June 30, 1958.

The calculations made above for phosphorus retention have been repeated for NO_3-N. Little Kitoi Lake retained about 22,400 kg NO_3-N and Upper Jennifer Lake 1,260 kg during the month of July. Dividing these quantities by the respective volumes of each lake, Little Kitoi Lake exhibits a net income of about 0.18 μg/L/day and Upper Jennifer Lake 0.009 μg/L/day, about 20 times less.

Phosphorus in watershed cores

Core samples of soil and ash were taken with a 24-in. steel sampling sleeve of 1.5-in. diameter attached to a driving head containing a ball check-valve. The sleeve was detached following each drive and an empty one used for each additional core. Cores were removed by placing the sleeve vertically upside-down in a vise. When the desired length had been pressed out with a hydraulic automobile jack, the sample was sliced off and placed in an aluminum weighing pan. Careful notes were made on the color and condition of each section. After drying, samples were passed through a 16-mesh sieve and transferred to jars for storage until analysis. In the field, a trench was dug to allow examination and measurement of the soil profile before the core was taken. Usually a photograph of the profile and of the surrounding vegetation was taken.

Twelve cores were obtained from the watersheds of the two lakes, four driven vertically and two driven perpendicularly to the slopes on Little Kitoi Lake, and an equal number in each category on Upper Jennifer Lake. The profiles showed the following features beginning with the uppermost layer: 1) litter consisting mostly of recently dead vegetation, 2) a layer of partially decomposed organic material, 3) a layer of fine white volcanic ash (more properly, tuff), 4) a layer of fine brown volcanic ash, 5) a layer of coarse white volcanic ash, 6) brown peaty material extending down to the limit of our cores (about 50 cm). The thickness of soil lying over the ash varied clearly with slope, from about 20 cm on the flat to 3 or 4 cm on a 45° slope. The total depth of ash averaged about 4 cm with varying but

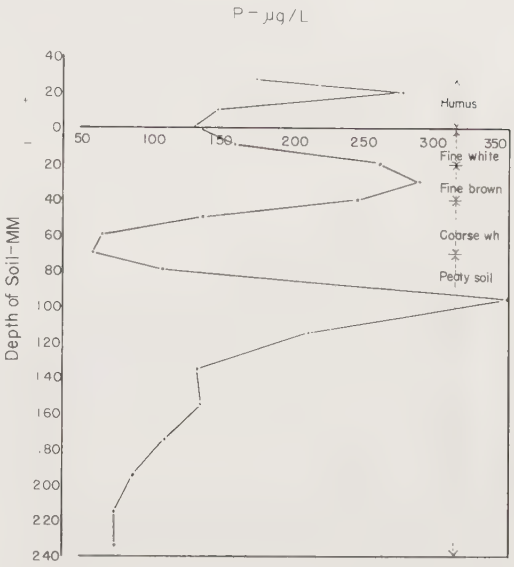

FIG. 4. Vertical distribution of acid-fluoride extractable phosphorus in a soil core taken high on a steep slope of Upper Jennifer Lake.

approximately equal thicknesses of each fraction. According to Griggs (1922) these layers represent three distinct ashfalls extending over a period of three days, from June 6 to 9, 1912. Each layer is easily recognized in a profile or in sections cut from a core.

Five vertical cores have been analyzed for phosphorus content by the method described above, four from Upper Jennifer and one from Little Kitoi. The five cores cover a range of slopes from 0–45° quite smoothly.

The data have been plotted by selecting the upper ash–soil interface for a datum plane, with initially no correction for slope. The curves plotted in this way show remarkable similarity. The most significant features can be seen in Figure 4, in which the vertical distribution of phosphorus in a core taken from the steepest slopes of Upper Jennifer is shown. Three peaks are usually present: 1) somewhere between the soil surface and the top of the ash, 2) within the fine brown ash or at the interface between this layer and the layer above or below it, and 3) in the peat not far below the bottom of the ash.

The factors operating to produce such a

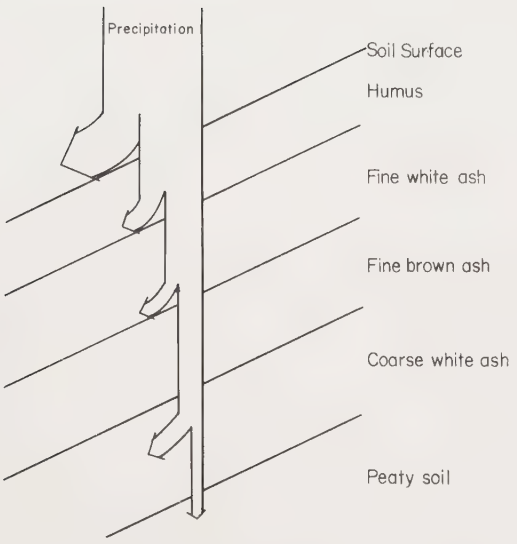

FIG. 5. Theoretical flow patterns on a watershed receiving Katmai ash.

complex distribution can be resolved by proceeding first with the assumption that the original phosphorus content of the ash showed no strong differences between layers (there are, to our knowledge, no analyses available for the individual layers of ash) and second, that the permeability of the various layers to water varies widely. A size-distribution of the ash particles has not been made, but there is no doubt that the middle, or fine brown, ash is extremely fine and forms a very compact layer, the fine white is coarser, and the coarse white or bottom layer has a very much larger particle size (our observations and also those of Griggs 1920). A diagram showing the way in which water derived from precipitation might be expected to behave is shown in Figure 5. Briefly, at each interface where a decrease in permeability to water is experienced, a partition of the water reaching that interface from above will occur, some of it tending to flow downward along the interface, and some seeping vertically under the influence of gravity into the next layer of material, and so on. The humus layer above the ash is highly permeable and we have supposed that the first two interfaces encountered by water moving downward show decreased permeability. The effect will be to divert a smaller absolute quantity of water at each interface. At the fine brown, coarse white ash interface the effect is altered since a more permeable layer is now encountered. The result is comparable to water dripping from a seam in the roof of a cavern. Most of the water getting this far will flow down through this channel since the next interface (with peaty soil) again decreases in permeability, probably to a very great extent. We are aware that this is an oversimplification, but believe that it does not seriously affect the basic conclusions.

This rather crude model explains the phosphorus curves shown by our cores with the additional assumption that the amount of phosphorus removed from a given point in the ash up to the present time is proportional to the amount of water which has moved past that point. Reference to Figure 5 shows that a relatively high flow rate should exist along the soil, fine white ash interface, and this appears as a minimum in Figure 4. Conversely, minimal flow is expected in the fine brown ash, and this is reflected by a maximum phosphorus content. A maximum flow is found again in the coarse white layer and is again reflected in a phosphorus minimum. The small amount of water moving into the subsoil produces the next phosphorus peak a short distance below the bottom of the ash. This accumulation layer might ordinarily be expected to occur deeper in the soil in a region with 60 in. of annual rainfall, but may be due to the impermeability of the ash or to its recent decomposition. The phosphorus peak occurring above the ash is almost certainly due to decomposition of organic matter in the surface layers. Several checks of this entire explanation can be made immediately:

1) If the coarse ash does indeed act as an underground watercourse, then the total flow within this layer must be higher near the bottom of a given watershed than near the top. A comparison of the phosphorus minimum in two cores taken along inlet 8 of Upper Jennifer (steep slope) shows 20 ppm in coarse ash taken near the stream mouth and 60 ppm in coarse ash taken about half-

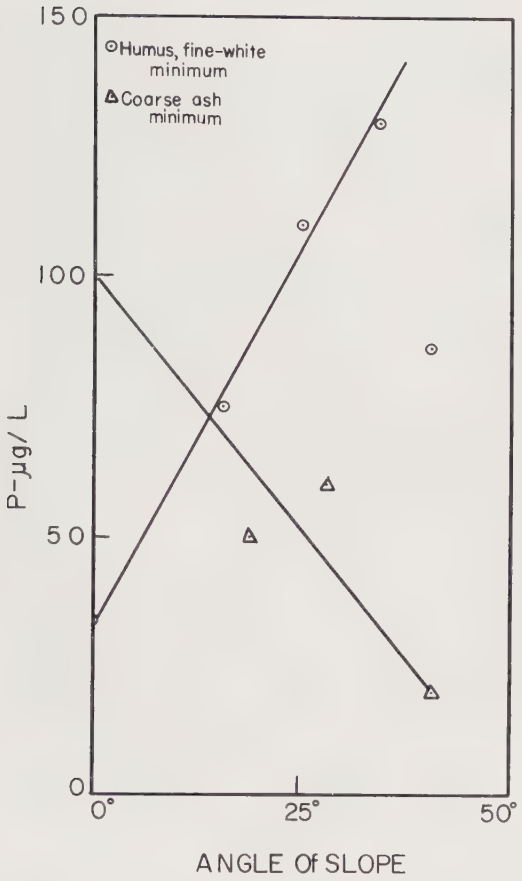

FIG. 6. Relationship between phosphorus content of minima appearing in the soil profile and slope.

way up the hill, as expected. Additional pairs of cores showed the same effects.

2) As the average slope of a watershed increases, the proportion of water running off the surface into the streams directly would be expected to increase. Proportionally, then, the flow along the soil–fine white ash interface will decrease, and the amount of phosphorus left should increase. Angle of slope is plotted against phosphorus concentration at this soil–ash interface in Figure 6; the points, with one exception, fall along a straight line with a positive slope.

3) In a single core, from the shallow slope along Upper Jennifer inlet 4, an additional layer of coarse white ash lies between the fine white, and fine brown layers. The theory predicts that practically no water would reach the subsoil under these conditions. The phosphorus analyses for this core (not shown) show that the subsoil accumulation peak is completely lacking.

4) In Figure 6 the phosphorus concentrations in the coarse ash minima have also been plotted against slope (omitting the aberrent core mentioned above). If our explanation is correct, it must be concluded that the flow rate within the coarse ash must increase with slope. The reason for this increased flow rate is not clear.

There seem to be no obvious contradictions to this general hypothesis, and the agreement with the tests which can be made at this point is good. It might be argued that we are dealing with an artificial situation brought about by using a particular analytical method, and that a completely different set of results might be obtained with a different extraction procedure. This is, of course, possible. However, according to Rankama and Sahama (1950) the phosphorus occurring in igneous rocks is usually present as small amounts of included apatite. The method used in this study extracts this mineral provided it is exposed to the solvent. In addition, it might be expected that at least with the acid portion of our extract we are duplicating in a much more severe way the extraction which goes on in nature. It is well known that acid soils would prevail in such a region and our measurements indicate a mean pH of about 5.5.

DISCUSSION

That the PO_4-P content of the inlet streams studied varies reciprocally with watershed slope has been shown. The model developed above to explain the manner in which phosphorus is leached from the Katmai ash is consistent with this observation. A steep slope appears to imply a decreased leaching rate at the soil–ash interface. (Although there is evidence of a high rate of leaching under these circumstances in the coarse-ash layer, this process appears to have been carried to the point where very little phosphorus remains.) Exactly opposite effect would presumably occur on shallow slopes and would tend to increase

the phosphorus concentration of the inlet waters. We recognize, of course, that some of the phosphorus found in the inlet streams comes from bacterial decomposition in the humus layer. It is also possible that an appreciable proportion is already present in the precipitation falling upon the watershed, although this seems unlikely according to information summarized by Hutchinson (1958, p 549).

Whatever the effect at the present time, it appears likely that the ash has contributed heavily to the phosphorus supply of the lakes in the past, particularly if the analysis of a mixed sample of ash, collected by Griggs prior to November, 1919 at Kodiak is correct. The phosphorus content (as P_2O_5), 3200 ppm, amounts to about 5 times the highest concentration we have found and about 20 times the levels of the interface minima. A great deal depends, of course, upon the time-rate of release, but a high initial rate is indicated by the sharp increase in growth rate of Sitka spruce near Kodiak, Kitoi Bay and Brooks Lake after the eruption, later followed by a decrease in growth rate.

Very little can be said at present about the actual effect of the two types of watersheds upon the primary productivity of the lakes. We have attempted to follow the seasonal course of primary production with the light and dark bottle method, meeting with little success (Dugdale and Wallace 1959). In one set of reliable measurements, however, Little Kitoi exhibited during mid-July an absolute rate of carbon fixation nearly twice that of Upper Jennifer Lake. Since, however, the mean chlorophyll *a* concentration in the euphotic zone of Little Kitoi Lake was also roughly twice that of Upper Jennifer, the gross photosynthetic rates become nearly equal when expressed in terms of chlorophyll *a* units present.

Our results point to a severe inorganic nitrogen deficiency in Upper Jennifer Lake. The lack of information regarding ammonia concentrations is unfortunate; it seems unlikely, however, that quantities in excess of the nitrate would be present. Juday, *et al.* (1932) found only traces of ammonia in the upper regions of Karluk influents; nitrate concentrations ranged from 5 to 40 μg/L. Both fractions increased toward the stream mouths, probably because of the presence of dead and decaying salmon. These "upper region" analyses are probably the most closely comparable to our data; the range of nitrate concentrations is nearly the same for both. This "upper region" water probably arose from recent precipitation and there are indications that very little ammonia or nitrate is present in the latter. Hutchinson (1958, p 552) gives 0.64 mg/L for the mean NH_4-N content of temperate rain water and 0.196 mg/L for the mean NO_3-N content. Data obtained from samples collected at Kitoi Bay and elsewhere in southern Alaska in 1960, and for which analyses are not entirely completed, indicate that NO_3-N is likely to occur in undetectably small amounts or at most about 15 μg/L, the former representing freshly collected rain water, the latter, old snow. The NH_4-N content of the three old snow samples analyzed so far ranged from 1.5–20 μg/L. These few data provide at least a hint that the quantities of these two nitrogen compounds occurring in southern Alaska precipitation may turn out to be very low, indeed.

Measurements of rate of primary nitrogen fixation within the two lakes were also made by us during the summer of 1958 (Dugdale, *et al.* 1959) using uptake of N^{15}. The rates obtained from these preliminary experiments suggest an upper limit of about 0.007 μg N/L/day, or about 0.003% newly fixed nitrogen per day for both lakes. This appears insignificant when compared to the rate of NO_3-N retention of Little Kitoi Lake, 0.18 μg/L/day but approximates the retention rate of Upper Jennifer Lake, 0.009 μg/L/day and may therefore be of considerable importance in the over-all nitrogen metabolism of the latter. Total nitrogen determined in conjunction with these experiments amounted to about 0.1 to 0.3 mg/L. No information is available regarding total or ammonia nitrogen retention.

The lakes of Afognak Island could probably be arranged in a spectrum; beginning with those surrounded by shallow restricted

watersheds, grading into those with greater proportions of steeper larger watersheds, and ending with those surrounded almost entirely by steep vast watersheds. The first would be expected to show severe nitrate deficiency, the condition becoming less severe with the accumulation of a greater proportion of steep watershed until achievement of balance somewhere toward the far end of the spectrum. Presumably a cline in primary productivity could also be observed to coincide. Whether such lakes exist, what modifications differing surface areas and depths would bring about, and whether our conclusions can actually be applied satisfactorily to other lakes remains to be examined in the future.

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SUN–ALTITUDE EFFECT ON THE DISTRIBUTION OF UNDERWATER LIGHT

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ABSTRACT

Skylighting which is symmetrical about the zenith generates a light vector diagram which is symmetrical about the vertical axis. When the sun departs from a position of symmetry the light vector diagrams become distorted. The extent of this distortion can to some extent be predicted from a knowledge of the scattering and reflecting properties of the water. The method of prediction is explained.

In homogeneous water, at a fixed depth, the distribution of light with azimuth angle in the horizontal plane will of course depend on the sun's altitude in the sky. If the sun is exactly at the zenith in a clear sky the light vector diagram for the horizontal plane will be a circle, that is, the magnitude of the flux will be a constant for all azimuths. If the sun were just below the horizon and the sky were clear, one would also expect that the horizontal light vector diagram would approach a circle of somewhat smaller magnitude than in the previous case. A truly circular light vector diagram would result in the latter case if the sky-dome exhibited a constant gradient from zenith to horizon at all azimuths, but this is not the case at sunset.

In between sunset and zenith-sun the horizontal light vector diagram is known to be pseudo-elliptical in shape (Johnson and Liljequist 1938; Whitney 1941; Sasaki *et al.* 1958). Thus, as the sun moves from the zenith to the horizon, the horizontal light vector diagram must stretch into a pseudo ellipse, attaining a maximum major axis at some intermediate sun angle and then shrink back again to a near circular shape at sunset.

Experimental data have recently been obtained by Sasaki and his co-workers (Sasaki *et al.* 1958) which demonstrate this sequence of changes in the horizontal light vector diagram.

The phenomena can be explained and the sun angle for maximum distortion of the light vector diagram can be predicted from fundamental hydro-optical considerations. There are two major factors which govern the shape of the horizontal light vector diagram. The first of these is intimately associated with the scattering function of the water. From Figure 1 it can be seen that as the sun sets and the angle of incidence, i, increases to 90°, the angle of refraction, r, increases to 48.6°, while θ (or 90° – r), decreases to 41.4°. Considering only the collimated light from the sun, the objective lens of the instrument, which is pointed horizontally, will face more and more into the forward lobe of the scattering from this collimated beam as the sun sets. The reading obtained will therefore increase more or less proportionately to the scattering function of the water and if nothing intervened would reach a maximum at sunset.

However, as i increases, the reflection of the air–water surface increases in accord-

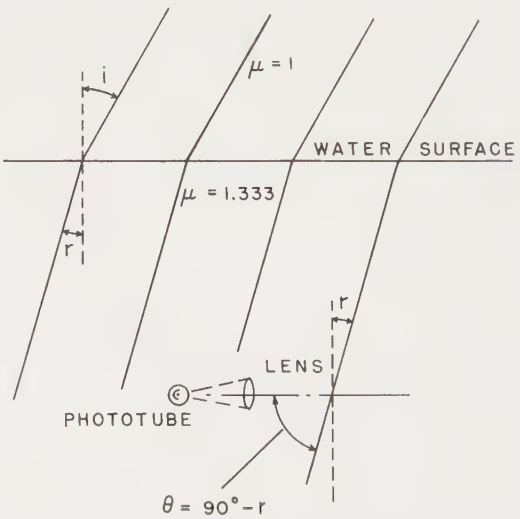

FIG. 1. Diagram illustrating the relationship between the scattering function of the water and the magnitude of the horizontal light vector in the direction of the sun.

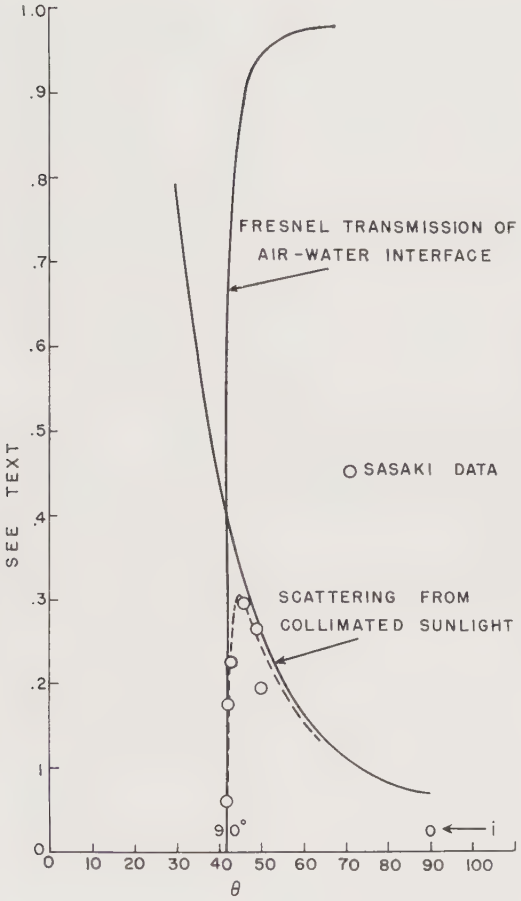

FIG. 2. Graphical illustration of the effect of scattering and of Fresnel transmission on the magnitude of the horizontal light vector in the direction of the sun.

ance with Fresnel's equations and the flux transmitted through the boundary decreases, finally reaching zero at $i = 90°$. The two effects are illustrated in Figure 2.[1] The Fresnel transmission data are plotted from 0 to 100% on the ordinate. The scattering function curve is taken from measurements of a water sample having an attenuation coefficient of 0.302/m, and a total scattering coefficient of 0.148/m. The directional scattering from the sun's collimated beam is assumed to be proportional to the shape of this scattering curve but the magnitude of the flux measured would be influenced by the depth at which measurements were made and by the volume of water involved. In the present problem Sasaki has measured the magnitude of the scattering and the scattering curve in Figure 2 is placed to conform with his maximum reading.

The horizontal flux measured in the direction of the sun as a function of i or θ will evidently be proportional to the product of these two curves, illustrated in Figure 2 by the dashed line.

From Figure 2 the maximum distension of the horizontal light vector diagram will occur when the sun is 70° from the zenith. The maximum distension reported by Sasaki occurred when the sun's angle from the zenith was 67.5°. Sasaki's normalized data are plotted in Figure 2 as circled points. In plotting these points the flux in the direction opposite to the sun has been subtracted since for normalized data this portion of the flux is not affected by the position of the sun.

This same phenomena should of course be observable at other angles than horizontal, and should be greatly exaggerated for observation angles less than 48° from the zenith.

[1] The Fresnel computations are here based on a flat interface. A roughened surface would no doubt alter the figures to some extent as would any change from the assumed scattering function of the water.

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NEGENTROPY FLOW IN COMMUNITIES OF PLANKTON[1]

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ABSTRACT

A model generalizing negentropy flux in plankton communities is presented. The biomass information equivalent $B(I)$ at time t is

$$B_t(I) = B_0(I) \exp [(\pi - \rho)/B(I)]\, t ,$$

where π (gross production) and ρ (respiration) represent rates of negentropy gain and loss, respectively. From this equation is derived an expression for the total community information in a homogeneous water column of depth z assuming a logistic relationship between photosynthesis and light intensity:

$$[B_t(\mathrm{I})]_{0\to z} = [B_0(I)]_{0\to z} \exp \phi\, I_0\, \delta^{-1} \{[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] - zc^{-1}\, [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}]\}\, t ,$$

where ϕ is a photosynthetic constant, I_0 is environmental negentropy concentration at the surface, δ is a decay coefficient expressing the rate of diminution of I_0 with depth, and c is the compensation depth. Various transformations of the exponent of this equation yielded for *gross production* in the whole water column:

$$(\pi)_{0\to z} = \rho c[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}]\, [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}]^{-1} ,$$

for *respiration*:

$$(\rho)_{0\to z} = \rho z ,$$

and for *net production*:

$$(\pi - \rho)_{0\to z} = \rho\{c[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}]\, [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}]^{-1} - z\} .$$

The *cost* in community negentropy to procure a unit of biotope negentropy was formulated as

$$(\rho/\pi)_{0\to z} = zc^{-1}[\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}]\, [\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}]^{-1} .$$

Empirical data are provided for a station in Raritan Bay which indicate a net loss of planktonic negentropy during the summer of 1959 amounting to 5.46×10^{20} bits/cm^2/day. A comparison of observed costs with expected values computed from the model indicated no significant difference between expectation and observation, demonstrating the efficacy of the model even under conditions where the assumption of perfect homogeneity throughout the water column was only partially realized.

INTRODUCTION

In a previous publication (Patten 1959), a model of ecosystem trophodynamics was presented against a background of modern developments in the theory of entropy. The classical statistical definition of entropy as the logarithm of the prior probability for occurrence of a particular state from an ensemble of equally probable states was given:

$$S = k \log P , \qquad (1)$$

where S is the entropy, k a constant, and P the probability. For systems with states of unequal probability, the corresponding expression is

$$S = k \sum_{i=1}^{n} p_i \log p_i , \qquad (2)$$

where p_i is the probability for the i-th permutation. Entropy is an extensive variable with a range $-\infty \leqslant S \leqslant +\infty$. The condition $S < 0$ qualifies for special attention: this "negative entropy" is regarded as conterminal with "information" (Brillouin 1951, 1956; Bell 1956), the subject of a special branch of statistics, *Information Theory*.

Besides a statistical interpretation, entropy is also reckoned in classical thermodynamics, the entropy change in a reversible process being expressed as

$$\Delta S = (S_t - S_0) = \int_0^t \frac{dQ}{T} dt , \qquad (3)$$

[1] Contributions of the Virginia Fisheries Laboratory No. 92.

where dQ is the rate of energy change, T is Kelvin temperature, and t is time. This equation posits null entropy change in reversible adiabatic transformations; therefore, states adiabatically accessible from one another must be regarded as informationally equivalent (Rothstein 1958). Conversely, states attainable only non-adiabatically are informationally different, and the energy fluxes associated with such transformations both imply and reflect corresponding entropy fluxes. This is equally true for so-called irreversible systems, which are reversible "in the limit" according to the principle of microscopic reversibility (Denbigh 1951).

Biological systems are regarded in cybernetics as self-organizing, self-regulating, and self-perpetuating automata—local enclaves of negative entropy in a universe overwhelmingly geared to a program of maximizing entropy. Such islands can only persist by continuously gulping huge quantities of negentropy from the environment (Schrödinger 1945). The equivalence of statistical and thermodynamic entropies provides a procedural basis for determining the rates at which information flows through biosystems (Patten 1959): namely by measuring energy fluxes under known temperature conditions, and then converting to entropy units.

This was done during the summer of 1959 for planktonic communities off Seguine Point, Staten Island in Raritan Bay in a series of 24-hr *in situ* dark and light bottle oxygen experiments. Complete details of the methods and an energetic analysis of the results are presented elsewhere (Patten 1960). Informational aspects are briefly summarized below following derivation of a model expressing productivity–depth relationships.

THE MODEL

Consider a water column perfectly homogeneous in every respect, both physical and biological. Let the total biomass of the entrained plankton at time t be regarded as a quantity of negative entropy, $B_t(I)$. Let π represent the rate of information gain by the community (gross production), and ρ be the rate of entropy generation (respiration):

$$\begin{aligned} \pi &= dB(I)^{+}/dt \\ \rho &= dB(I)^{-}/dt , \end{aligned} \tag{4}$$

with the resultant

$$\frac{dB_t(I)}{dt} = \pi - \rho , \tag{5}$$

the net production. Assuming the rates of accrual and attrition to be proportional to $B(I)$, then

$$\frac{dB_t(I)}{dt} = v\,[B(I)] , \tag{6}$$

where v is a constant expressing the net production per unit of biomass

$$v = \frac{\pi - \rho}{B(I)} .$$

Solving (6) by separating the variables and integrating gives

$$\begin{aligned} B_t(I) &= Ce^{vt} \\ &= C \exp\,[(\pi-\rho)/B(I)]\; t . \end{aligned}$$

Setting the integration constant equal to the initial negentropy of the community, we obtain

$$\boxed{B_t(I) = B_0(I) \exp\,[(\pi-\rho)/B(I)]\; t} \tag{7}$$

for the total information equivalent of the community at time t.

In a uniform water column, the rate of negentropy loss per unit biomass is constant at all depth, z:

$$[\rho/B(I)]_z = \lambda \tag{8}$$

Negentropy accumulation, on the other hand, is inconstant with depth since it depends upon solar radiation which is extinguished exponentially. A general accrual function may be represented by:

$$[\pi/B(I)]_z = \Phi(I_z) . \tag{9}$$

This function may take at least three specific forms depending upon the kind of relationship which exists between photosynthesis and light intensity. Photosynthesis has been widely demonstrated to bear a linear correspondence with light intensity under conditions of low and moderate illuminance. Under these circumstances (case I), Φ

would be a simple exponential function paralleling light extinction:

$$\Phi = \phi I_z = \phi I_0 e^{-\delta z} , \qquad (10)$$

where ϕ is a proportionality constant, and δ expresses the rate of negentropy decay. A model based on (10) is given elsewhere (Patten 1960). It is necessarily unrealistic at higher light intensities where the connection between production and illumination becomes less than linear (see, for example, Myers 1953 and Ryther 1959). In this case (II), a logistic relationship between photosynthesis and light intensity may be presumed, which leads to a correspondence between photosynthesis and depth which is likewise sigmoid:

$$\Phi = \phi I_0 e^{-\delta z}(1 - \pi_z \pi_{\max}^{-1}) , \qquad (11)$$

where $\pi_{\max}$ is the upper asymptote of production. The model formulated below is based on this relationship. A third case (III) arises when illumination intensities become so high as to actually inhibit photosynthesis (Ryther 1956, and others). No satisfactory expression for Φ under these conditions is manifest at the present time; however, it may be remarked that from the standpoint of the whole water mass case III is almost tautological since the condition can only prevail in the upper few centimeters of all but the most transparent of natural waters (which are biologically void anyway).

Substitution of equations (8) and (11) into (7) yields

$$[B_t(I)]_z = [B_0(I)]_z \exp [\phi I_0 e^{-\delta z}(1 - \pi_z \pi_{\max}^{-1}) - \lambda] t ,$$

or for the whole water column:

$$[B_t(I)]_{0\to z} = [B_0(I)]_{0\to z} \exp \{ \int_0^z [\phi I_0 e^{-\delta z}(1 - \pi_z \cdot \pi_{\max}^{-1}) - \lambda] dz \} t . \qquad (12)$$

The expression $(1 - \pi_z \pi_{\max}^{-1})$ may be converted to an integrable form by noticing (equation 9) that

$$\pi_z = B_z \Phi = B_z \phi I_0 e^{-\delta z} ,$$

and that

$$\pi_{\max} = \pi_{z=0} = B_0 \phi I_0 .$$

Thus,

$$\pi_z \pi_{\max}^{-1} = B_z \phi I_0 e^{-\delta z} / B_0 \phi I_0$$

which cancels (since $B_z = B_0$ in a uniform water column) to the form

$$\pi_z \pi_{\max}^{-1} = e^{-\delta z} . \qquad (13)$$

Substituting this into (12) results in

$$[B_t(I)]_{0\to z} = [B_0(I)]_{0\to z} \exp \{ \int_0^z [\phi I_0 e^{-\delta z}(1 - e^{-\delta z}) - \lambda] dz \} t ,$$

which may be readily integrated to produce

$$[B_t(I)]_{0\to z} = [B_0(I)]_{0\to z} \exp \{ \phi I_0 \delta^{-1} [\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] - \lambda z \} t . \qquad (14)$$

In this expression, the left term of the exponent denotes the rate of trophogenesis per unit biomass, and the right term tropholytic rate per biomass unit in the total water column.

A further simplification may be obtained by considering the concept of compensation. Since π diminishes exponentially with depth while ρ remains constant (Sverdrup 1953), then given $\pi > \rho$ at the surface and a long enough water column, there must exist some depth $z = c$ above which $\pi > \rho$, below which $\pi < \rho$, and at which $\pi = \rho$. This is the *compensation depth*, at which the concentration of environmental negentropy constitutes the *compensation point*. At $z = c$, the exponent of equation (14) must vanish:

$$\phi I_0 \delta^{-1} [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}] - \lambda c = 0 .$$

This constraint permits λ to be expressed as

$$\lambda = \phi I_0 \delta^{-1} c^{-1} [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}] . \qquad (15)$$

Since the water column is homogeneous and λ is constant at all levels, (14) may be rewritten

$$\boxed{[B_t(I)]_{0\to z} = [B_0(I)]_{0\to z} \exp \{ \phi I_0 \delta^{-1} \{ [\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] - z c^{-1} [\tfrac{1}{2}(1 + e^{-2\delta c}) - e^{-\delta c}] \} t} \qquad (16)$$

In this expression gross production is represented as

TABLE 1. *Negentropy fluxes in Raritan Bay, summer 1959. All flow rates are expressed as (bits × 10^n)/cm^2/day, and efficiencies as bits/bit.*

Expt.	Dates	$(I)_{0\to z}$ (bits × 10^{-22})	$(\pi)_{0\to z}$ (bits × 10^{-20})	$(\rho)_{0\to z}$ (bits × 10^{-20})	$(\pi-\rho)_{0\to z}$ (bits × 10^{-20})	$(\pi/I)_{0\to z}$ (bits/bit)	$(\rho/\pi)_{0\to z}$ (bits/bit) Observed	Expected
I	Jun 16–17	18.64	11.48	15.42	–3.94	.00616	1.34	1.35
II	Jun 23–24	26.25	27.60	14.95	12.65	.01051	0.54	1.74
III	Jul 2–3	20.75	14.57	23.45	–8.88	.00702	1.61	2.01
IV	Jul 8–9	26.11	44.72	30.15	14.57	.01713	0.67	1.92
V	Jul 15–16	10.00	6.86	13.83	–6.97	.00686	2.02	1.10
VI	Jul 20–21	21.96	5.27	6.30	–1.03	.00240	1.20	0.92
VII	Jul 29–30	10.98	31.56	78.54	–46.98	.02873	2.49	2.32
VIII	Aug 3–4	43.18	24.29	27.28	–2.99	.00563	1.12	1.22
IX	Aug 10–11	34.98	19.61	31.03	–11.42	.00561	1.58	0.96
X	Aug 17–18	20.91	18.43	20.80	–2.37	.00881	1.13	1.11
XI	Aug 24–25	18.41	1.83	4.58	–2.75	.00099	2.50	∞
Means			18.75	24.21	–5.46	.00908	1.29	

$$(\pi)_{0\to z}=\phi I_0\delta^{-1}\left[\tfrac{1}{2}(1+e^{-2\delta z})-e^{-\delta z}\right]\left[B(I)\right],$$

and respiration is

$$(\rho)_{0\to z}=\phi I_0\delta^{-1}zc^{-1}\left[\tfrac{1}{2}(1+e^{-2\delta c})-e^{-\delta c}\right]\left[B(I)\right].$$

Since, from (15),

$$\phi=\lambda I_0^{-1}\delta c\left[\tfrac{1}{2}\left(1+e^{-2\delta c}\right)-e^{-\delta c}\right]^{-1},$$

and, from (8), $\lambda=\rho/B(I)$, these expressions can be transformed to

$$\boxed{(\pi)_{0\to z}=\rho c\left[\tfrac{1}{2}(1+e^{-2\delta z})-e^{-\delta z}\right]\left[\tfrac{1}{2}(1+e^{-2\delta c})-e^{-\delta c}\right]^{-1}} \qquad (17)$$

for gross production,

$$\boxed{(\rho)_{0\to z}=\rho z} \qquad (18)$$

for respiration, and

$$\boxed{(\pi-\rho)_{0\to z}=\rho\left\{c\left[\tfrac{1}{2}(1+e^{-2\delta z})-e^{-\delta z}\right]\left[\tfrac{1}{2}(1+e^{-2\delta c})-e^{-\delta c}\right]^{-1}-z\right\}} \qquad (19)$$

for net production in the whole water column.

An additional variable, of interest because it is intensive rather than extensive like the production variables, is *cost*, the amount of community information expended to procure a unit of environmental negentropy:

$$\boxed{(\rho/\pi)_{0\to z}=zc^{-1}\left[\tfrac{1}{2}\left(1+e^{-2\delta c}\right)-e^{-\delta c}\right]\left[\tfrac{1}{2}(1+e^{-2\delta z})-e^{-\delta z}\right]^{-1}} \qquad (20)$$

This cost factor both reflects and determines the dynamic state of the ecosystem in any interval of time:

$$\begin{array}{ll}\rho/\pi=1 & \text{(steady state)}\\ \rho/\pi<1 & \text{(growth)}\\ \rho/\pi>1 & \text{(regression)}\end{array} \qquad (21)$$

APPLICATION TO RARITAN BAY

A major drawback to the modeling approach derives from the inherent complexity of biological systems. A formulation, if it is not to be unwieldy, must be based upon one or more simplifying assumptions. With the foregoing model, only three easily measured parameters (z, c, and δ) are needed to evaluate community costs—in "perfectly homogeneous" waters.

The Raritan Bay station occupied during the summer of 1959, although reasonably uniform with respect to temperature and salinity, was decidedly stratified biologically, especially in early experiments when motile flagellates dominated the flora. This heterogeneity was reflected in respiration–depth curves, which often negated the assertion of equation (18). The empirical data obtained are summarized in Table 1. They denote that due to the high cost (mean: 1.29 bits/bit) and low efficiency (mean: 0.908%) of extracting information from the biotope, a mean daily entropy gain was sustained by the plankton amounting to 5.46 ×

10^{20} bits/cm^2. The implications of this are considered elsewhere (Patten 1960).

To evaluate the efficacy of the model, expected costs were calculated from equation (20) utilizing white light extinction coefficients determined with a Lumetron colorimeter (and corrected for non-collimation *in situ*) and compensation depths obtained experimentally. These figures appear in Table 1 opposite the empirical costs. To test the contingency between observed and expected values, the probability $P(D_n > T_\alpha|$ equation (20 is the correct distribution function) was determined where D_n is the Kolmogorov-Smirnov statistic (Whitney 1959) denoting the maximum deviation between observed and predicted, and T is the table value for the D_n distribution at the probability level α. If $D_n > T_\alpha$, the hypothesis of contingency is rejected, whereas if $D_n \leq T_\alpha$, the hypothesis is accepted at the level of significance α. D_n was computed to be 0.182; T at $\alpha = .01$ is 0.468. Hence the experimental results were the same as those predicted by equation (20) on a significance level of 1%, and it may be concluded that the mathematical model is isomorphic with the observed flux of negative entropy in the summer plankton of Raritan Bay.

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A BIOLOGICAL ASSAY FOR THIAMINE IN SEA WATER[1]

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ABSTRACT

A non-filamentous marine phycomycete, isolate S-3, responds in a quantitative and specific manner to the presence of thiamine. This fungus has been used to assay for thiamine in sea water. The assay is sensitive to 25 $\mu\mu$g/ml thiamine.

Thiamine auxotrophy is a characteristic of all of the 39 isolates of non-filamentous marine Phycomycetes currently growing on synthetic media in our laboratory, as well as of some marine phytoflagellates (Droop 1958, Provasoli 1958). The concentration and distribution patterns of thiamine in sea water may therefore be of ecological importance. Since no direct assay method was available for the determination of thiamine in sea water, one of these auxotrophic fungi has been developed as an assay organism. Provasoli and Gold (1959) have recently suggested the use of *Gyrodinium cohnii*, a dinoflagellate which appears to be less sensitive to thiamine. The results of our assays of Long Island Sound waters are the subject of a separate paper (Vishniac 1961).

METHODS

The fungus chosen was isolate S-3, obtained by our usual procedures (Vishniac 1955) from sea water used in clam cultures at the Milford Station of the U. S. Fish and Wildlife Service received on 10 February 1954 through the courtesy of Dr. Victor Loosanoff. Four similar isolates, of which one is still maintained, were obtained from water received 1 October 1954. In culture this fungus consists of small (4–13 μ) thin-walled spheres, containing refractile granules, not obviously vacuolate, apparently lacking rhizoids, becoming bright orange-red with age. Zoospore liberation has not been observed, though an abundance of zoospores is produced. Electron micrographs taken through the courtesy of Dr. William Gaylord have shown that the zoospores are heterokont. This isolate is therefore presumably a member of the Ectrogellaceae. It is regretable that the observations necessary to classify this isolate systematically have not been made. That they have not is, in part, a reflection on the nature of taxonomic descriptions of the archimycetous marine phycomycetes in general. It is our conviction that considerable experimental morphology and correlation of cultural characteristics with those observed in material collected from nature will be necessary to clarify the systematics of this ecological group to the extent that a specific designation will be useful to the physiologist.

Of the isolates available, S-3 was chosen for its ease of culture. S-3 tolerates a wide range of salinity and temperature, growing rapidly to Klett readings of 250 or more (#42 filter) with autoclavable substrates, and is almost unique among our isolates in requiring only thiamine as a growth factor. The stock medium (Table 1) currently in use for maintenance, and with the omission of thiamine and glucose as a basal medium for the assay, was developed for general use with non-filamentous marine phycomycetes through experiments with other isolates. Preliminary experiments with S-3 itself, as well as our assay experience, have indicated the suitability of this medium and of the cultural conditions used for S-3. Growth was possible at temperatures ranging from at least 15° to 36°C and was optimal at 30°. Viability was maintained for at least a month under ordinary refrigeration. S-3 did

[1] The preliminary experiments on the response of S-3 to thiamine were performed by Mr. J. Fedors and Mr. T. Yamamoto, whom we wish to thank for their interest and enthusiasm. The technical assistance of Miss J. Wertz and Miss J. Pumphrey has been most valuable. The study was assisted by Grant E1179 from the National Institute of Allergy and Infectious Diseases, National Institutes of Health, Public Health Service.

TABLE 1. *Stock medium for fungus S-3*

Salts (5× solution yielding final concentrations of)	
NaCl	2.5 %
$MgSO_4.7\ H_2O$	0.5 %
KCl	0.1 %
KH_2PO_4	0.01%
$CaCO_3$	0.02%
H_2SO_4 to dissolve	
$(NH_4)_2SO_4$	0.02%
NaOH to pH *ca.*	6.0
Trace Metals (100× solution yielding final concentrations of)	
Na_2 EDTA	5.0 mg/100 ml
Fe^{++} (as $FeSO_4.7H_2O$)	0.05 mg/100 ml
Zn^{++} (as $ZnSO_4.7H_2O$)	0.02 mg/100 ml
Mn^{++} (as $MnSO_4.H_2O$)	0.01 mg/100 ml
Co^{++} (as $CoSO_4.7H_2O$)	2.0 μg/100 ml
Cu^{++} (as $CuSO_4.5H_2O$)	0.2 μg/100 ml
B^{+3} (as H_3BO_3)	2.0 μg/100 ml
Mo^{+6} (as $Na_2MoO_4.2H_2O$)	2.0 μg/100 ml
and	
NaH. glutamate 0.2%	
Glycerol 0.2%	pH 7.5 (NaOH)
Agar 0.1%	
Thiamine. HCl 1 μg/100 ml	
Glucose (filter sterilized and added to sterile medium) 0.2%	

not grow in the absence of NaCl, and grew maximally in the presence of 2% to at least 5% NaCl. $MgSO_4.7H_2O$ at 0.5% is in excess of the lowest concentration (0.1%) which will support maximal growth. Concentrations of $CaCO_3$ higher than in the stock medium favored greater growth but resulted in the formation of precipitates which slowly disappeared during growth. Alanine, serine, NaH.glutamate, and to a lesser extent isoleucine and valine supported growth as sole carbon sources. Glycerol and Na.acetate.$3H_2O$, but not soluble starch, sucrose, ethanol, mannitol, lactate, gluconate, succinate, or citrate, were available substrates in the presence of limiting amounts of gelatin hydrolysate. Glycerol alone will support some growth, but this growth is improved by the addition of Na.H.glutamate or Na_2.succinate.$6H_2O$ to the medium. Raising the concentration of glycerol and glutamate given in the stock medium to 0.5% each did not increase growth.

The thiamine requirement of S-3 was discovered by the usual method of growing the organism in media lacking vitamins until it failed to grow well, then using such a culture as inoculum for media containing various known vitamins and mixtures of vitamins. The requirement is specific for thiamine; S-3 did not respond to either 4-methyl-5β-hydroxyethyl thiazole or 2-methyl-4-amino-5-ethoxymethyl pyrimidine (obtained through the courtesy of Dr. K. Folkers and Dr. H. B. Woodruff) alone or in combination at concentrations up to 500 $\mu\mu$g/ml.

Preparation of media

All solutions and media prepared from them were made with glass-distilled water either freshly prepared or preserved with Hutner's volatile preservative, as were the solutions themselves. Mallinckrodt AR and Nutritional Biochemical Company chemicals were used. Thiamine stock solutions (1 ml = 100 μg) were prepared in 0.01 N HCl and kept frozen until dilution and immediate use. Glassware was washed by rinsing and boiling for ½ hr with a commercial detergent, rinsed 6 times after the visible disappearance of detergent with tap water and 3 times with distilled water. Glassware contaminated with concentrations of thiamine higher than 10 $\mu\mu$g/ml were segregated and subjected to the complete washing procedure twice before reuse. A single washing was insufficient to remove detectable thiamine from beakers experimentally contaminated with 10 times this concentration, though beakers contaminated with 2 times this concentration were effectively cleaned. Pipettes were plugged with glass wool and sterilized in copper containers to avoid contamination with thiamine from materials of biological origin. The basal medium (Table 1 with the omission of thiamine and glucose) was made up in half the final volume, adjusted with NaOH to the pH given, brought to boiling to dissolve the agar, and brought to final volume after cooling. The medium was dispensed in 5-ml lots into 16 × 125 mm screw-capped tubes with teflon liners for use for culture maintenance and inoculum production and in 10-ml lots into 25-ml pyrex Erlenmeyer flasks capped with pyrex beakers for use for standard curves and assays. The Erlenmeyer flasks

were subsequently enclosed between two pyrex kitchen trays. Media were autoclaved for 10 min, cooled in the autoclave for 15 min, and removed to a cold room until cool enough to inoculate. While the time of autoclaving is itself not a variable in comparing standard and assay responses, it was considered possible that destruction of thiamine during autoclaving might occur at the pH employed. There was, however, no increased response when limiting amounts of (sintered glass filter-sterilized) thiamine were added aseptically after autoclaving rather than before autoclaving. An unfortunate occurrence, however, made us aware that longer autoclaving, of 25 min duration, results in appreciable thiamine destruction.

Preparation of inocula

When S-3 is transferred from stock culture to tubes of medium to which thiamine has not been added, using 10% inocula and subculturing at weekly intervals at room temperature, the third subculture makes barely visible growth and is thiamine depleted. Thereafter 20% subcultures were made into both thiamineless and complete media to assure viability of the culture. The barely visible growth which continues to appear is complete in 2 to 3 days, after which the culture may be used as inoculum. The use of cultures 5 to 6 days old does not appear to alter the results of the experiment in any way. The use of a minimal amount of thiamine (20 $\mu\mu$g/ml) in the depletion tubes increased the time required for inoculum growth and, although the larger population produced results in a decreased lag phase in assays, the final results of the assay were not affected. Concentrating the inoculum by centrifugation is impractical because of the agar in the medium. It was not necessary, indeed it would be undesirable, to prepare thiamine-free agar for the preparation of inocula and media, since the level of growth supported by the present depletion medium has remained constant and useful through at least 33 serial transfers.

Preparation of sea water samples

Sea water samples collected with a Nansen bottle were immediately filtered through millipore HA or AA filters into 6-oz polyethylene bottles and frozen with dry ice. The filtration apparatus and procedure used on shipboard have been used in the laboratory to filter synthetic medium (lacking agar) to which 200 $\mu\mu$g thiamine/ml were added. There was no difference in the response of S-3 to aliquots of this medium which had been filtered and those which had not been filtered. The frozen samples were stored in a dry ice chest until use. The ability of thiamine to withstand this storage procedure was tested with pooled old samples of known low thiamine content to which 500 $\mu\mu$g thiamine/ml were added. The pool was then divided into 5 aliquots which were stored as usual and have been assayed approximately 2 weeks and 3 months after preparation. The thiamine content was unchanged at the time of the last assay (Klett readings at 2 weeks 83, 83; at 3 months 84.5, 86.5). Hutner's volatile preservative was added to the samples on collection or just before thawing for use.

For assay, 100 ml of sea water is thawed rapidly by shaking and immersion in tepid water. It is then enriched with 1 ml of a metal mixture to provide chelator and metals at the final concentration of the synthetic medium, and with 1 or 2 ml of solutions to provide 10 mg of $(NH_4)_2SO_4$, 0.2 g of NaH.glutamate and 0.2 g of glycerol. Agar, 0.1 g, is dissolved during a total of 6 min heating, following which the sample is restored to 100 ml with vitamin-free glass-distilled water. When thiamine was added to synthetic medium before the solution of agar, as in assaying sea water samples, there was no decrease in the response of S-3 as compared to the results of the standard curve in synthetic medium which is prepared by first dissolving the agar and subsequently adding appropriate amounts of thiamine.

The enriched sea water samples are then distributed in duplicate 10 ml aliquots in 25 ml Erlenmeyers. A second series of duplicate aliquots is distributed after the addition of 100 $\mu\mu$g thiamine/ml (in 0.1 ml/10ml) for the estimation of vitamin recovery. Sterilization procedures were as outlined for syn-

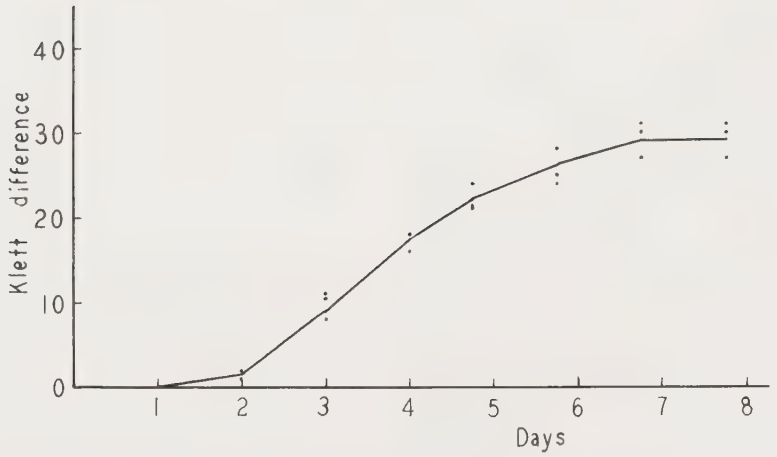

FIG. 1. Time course of growth of S-3 with limiting thiamine (200 $\mu\mu$g/ml). Incubated at 25°C.

thetic media. The sterile samples are then further enriched by the aseptic addition of 0.1 ml of 0.5% KH_2PO_4 and inoculated with one drop of inoculum.

The assay

Each series of enriched sea water samples is accompanied by a standard curve for thiamine in synthetic medium to which has been

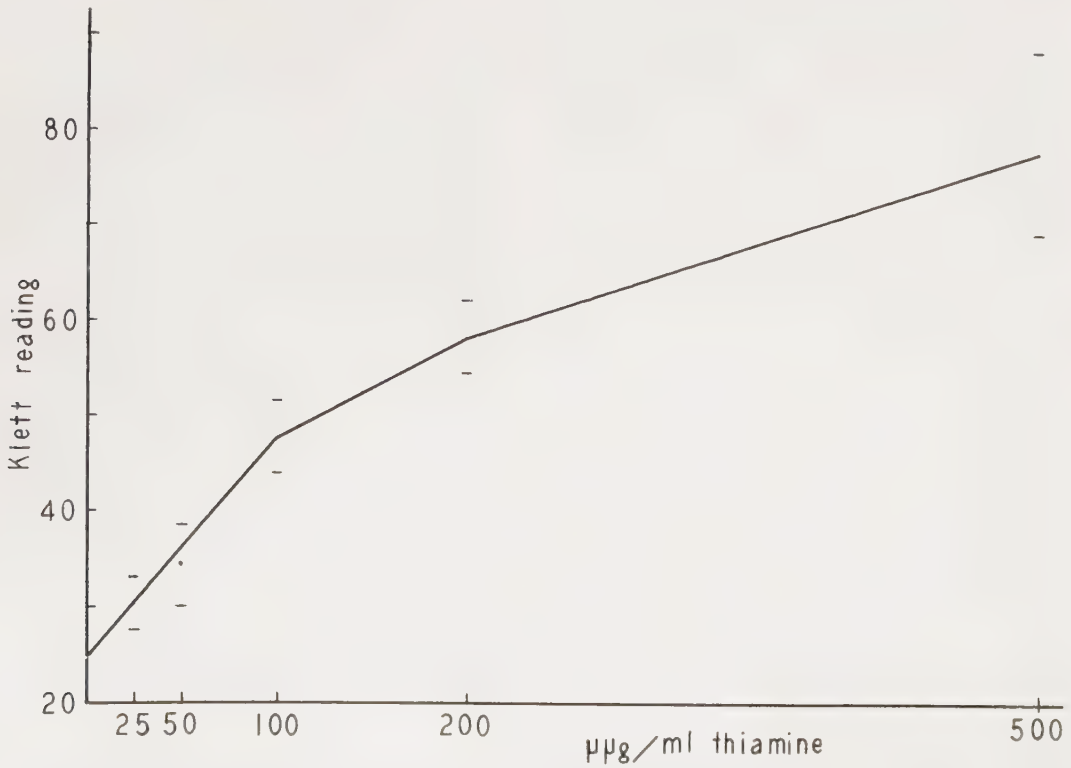

FIG. 2. Response of S-3 to thiamine. Points are averages of three experiments performed in duplicate; dashes indicate the highest and lowest values obtained.

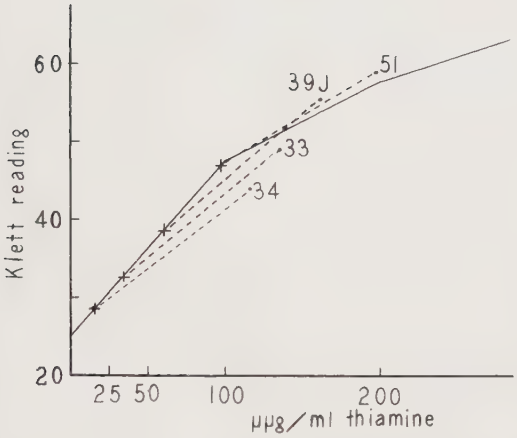

FIG. 3. The assay results of samples 33, 34, 39J, and 51 with (.) and without (+) added thiamine (*ca.* 100 μμg/ml), projected onto the standard response curve.

added 0, 25, 50, 100, 200, or 500 μμg thiamine/ml. The inoculated preparations are incubated for 7 days in a refrigerated incubator at 25°C. The trays are gently shaken every second day to ensure even distribution of growth. The length of incubation necessary is determined by following the time course of growth (Figure 1) in 10 and 25 ml of medium distributed in 25- and 125-ml Erlenmeyers to which has been fused a Klett tube so that the contents can be examined colorimetrically without disturbing the course of growth. Growth was substantially complete in 7 days. Such experiments and assays were read with a Klett-Summerson photoelectric colorimeter with #42 filter.

RESULTS

The readings thus obtained were converted into concentrations of thiamine by comparison with the standard curve of Figure 2. This curve was plotted from the average of three experiments, each performed in duplicate. We have been unsuccessful in decreasing the unfortunately high interexperimental variation shown in Figure 2. However, the close agreement obtained in the assay of stored sea water with added thiamine suggests that this degree of variation may not occur in sea water media. The results of representative actual assays shown in Figure 3, together with the recoveries of thiamine added to duplicate aliquots for assay, are given to indicate roughly the accuracy obtained by referring sample readings to the standard curve.

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COBALAMIN AND THIAMINE IN LONG ISLAND SOUND: PATTERNS OF DISTRIBUTION AND ECOLOGICAL SIGNIFICANCE[1]

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ABSTRACT

Cobalamin occurs in surface waters of Long Island Sound at high levels (to 16 $\mu\mu$g/ml) during the winter, falling markedly with the late winter diatom bloom and rising during the summer with temperature. The pattern of cobalamin and PO_4-P concentrations are similar, both nutrients reflecting but not limiting phytoplankton growth. Thiamine is present only in barely detectable amounts in the main body of the Sound. Data suggest that thiamine, but not cobalamin, may be mainly derived from land drainage.

INTRODUCTION

None of the types of information necessary to determine the significance of growth factors in marine ecology is presently adequate. We know, from the research of several laboratories, that many of the littoral phytoplankton (Provasoli 1958, Droop 1958, 1959), non-filamentous fungi (unpublished data from our laboratory), and some of the bacteria (Burkholder 1959) require organic growth factors. We do not know how to cultivate the strictly oceanic phytoplankton. Nor do we know the effects of low but constant concentrations of growth factors on culturable species, though the studies of Ford (1958) on the fresh-water species *Ochromonas malhamensis* represent an admirable approach to such information. Are these growth factors present in the ocean? The toxicity of sea water for the usual assay organisms has prevented their general application to this habitat. It is possible to assay sea water for cobalamin with *E. coli* mutants or *Euglena* following extraction of the vitamin (Cowey 1956), desalting or dialysis (Provasoli and Pintner 1953, Kashiwada *et al.* 1956, 1957) or dilution (Daisley 1958), or directly using marine microorganisms (Droop 1955, Adair and Vishniac 1958). Direct methods for the assay of other growth factors are suggested by the studies of Belser (1959), Burkholder (1959), and Provasoli and Gold (1959), but these have not been extensively used. Even for cobalamin, we do not yet have a broad picture of its distribution in terms of both cyanocobalamin and related factors, or knowledge of the variables which influence their concentration in a given natural situation. For these reasons, finding ourselves in possession of organisms which could be used for the direct assay of cobalamin (Adair and Vishniac 1958) and thiamine (Vishniac 1961) in sea water, we have undertaken a study of the seasonal variation in the concentration of these vitamins in Long Island Sound, a body of water concerning which a variety of other information was readily available. It soon became apparent that Long Island Sound possessed a further advantage in that the concentration of cobalamin was usually within such a range that significant correlations of changes which environmental variables could easily be found. There are two main unsatisfactory aspects of such studies: first, that they can only show correlations which require experimental studies for complete understanding; secondly, that they are limited by the specificity of the assay used.

METHODS

The assay organisms used routinely in our laboratory are the non-filamentous fungi (phycomycetes) *Thraustochytrium globosum* for cobalamin (Adair and Vishniac 1958) and the unidentified isolate S-3 for

[1] This study was assisted by a research grant, E1179 from the National Institute of Allergy and Infectious Diseases, National Institutes of Health, Public Health Service. We are grateful for the excellent technical assistance of Miss J. Wertz and Miss J. Pumphrey.

TABLE 1. *Basal medium*

Salts (5× solution yielding final concentrations of)	
NaCl	2.5 %
$MgSO_4.7\ H_2O$	0.5 %
KCl	0.1 %
KH_2PO_4	0.01%
$CaCO_3$	0.02%
H_2SO_4 to dissolve	
$(NH_4)_2SO_4$	0.02%
NaOH to pH *ca.* 6.0	
Trace Metals M-5 (100× solution yielding final concentration of)	
Na_2EDTA	5.0 mg/100 ml
Fe^{++} (as $FeSO_4.7H_2O$)	0.05 mg/100 ml
Zn^{++} (as $ZnSO_4.7H_2O$)	0.02 mg/100 ml
Mn^{++} (as $MnSO_4.H_2O$)	0.01 mg/100 ml
Co^{++} (as $CoSO_4.7H_2O$)	2.0 μg/100 ml
Cu^{++} (as $CuSO_4.5H_2O$)	0.2 μg/100 ml
B^{+3} (as H_3BO_3)	2.0 μg/100 ml
Mo^{+6} (as $Na_2MoO_4.2H_2O$)	2.0 μg/100 ml
and	
NaH. glutamate 0.2%	
Glycerol 0.2%	pH 7.5 (NaOH)
Agar 0.1%	
Thiamine. HCl 1 μg/100 ml	
Glucose (filter sterilized and added to sterile medium) 0.2%	
$NaHCO_3$ (autoclaved and added to sterile medium) 0.02%	

thiamine (Vishniac 1961). *Thraustochytrium globosum* responds only to cyanocybalamin and $B_{12\ III}$. S-3 requires intact thiamine. Both are sensitive (to less than 1.0 μμg/ml cobalamin and to approximately 20 μμg/ml thiamine), grow fairly rapidly (within 11 and 7 days respectively at 25°C) in simple media in the absence of light. Both are obligately marine and usually do well in sea water appropriately enriched for direct assay. Some samples of winter sea water (24 November 1958, 8 January 1959) were toxic for *Th. globosum*; 1:4 dilutions of these samples were no longer inhibitory.

The conditions used by Adair and Vishniac were modified in the course of our study. The basal medium used for determining the response of *Th. globosum* to cobalamin is given in Table 1. The standards and assays were incubated at 25°C, rather than 15°C, for 11 days. The response of *Th. globosum* under these conditions, averaged from 7 experiments run in duplicate, is shown in Figure 1. This response was reasonably constant for the period of the assays reported here. At a later date the fungus ceased to respond to cobalamin unless yeast extract (10 mg/100 ml) was added to the medium. This response was not commensurate with the response to cobalamin in enriched sea water, however, so the assay ceased to be useful.

FIG. 1. Response of *Th. globosum* to vitamin B_{12}.

The assay procedure consists of enriching 100 ml of rapidly thawed sea water with metal mixture M-5 (Table 1), $(NH_4)_2SO_4$, 10 mg; NaH glutamate, 0.2 g; and glycerol, 0.2 g. Agar, 0.1 g, is dissolved during a total of 6 min heating to boiling, following which the volume of sample is restored to 100 ml

with vitamin-free glass-distilled water. Duplicate 10-ml aliquots are distributed in 25-ml Erlenmeyers for assay. Thiamine is assayed without dilution. Cobalamin is assayed with and without 1:4 dilution with vitamin-free synthetic medium, after the addition of 1 μg/100 ml of thiamine. Another series of duplicate aliquots is distributed with the addition of 100 $\mu\mu$g/ml cobalamin for the estimation of vitamin recovery. After sterilization for 10 min followed by rapid cooling, aseptic additions are made of filter-sterilized glucose (0.1 ml to yield a final concentration of 0.2%) for cobalamin assay, KH_2PO_4 (0.1 ml to yield 0.005%) for undiluted sea water assays, and $NaHCO_3$ (0.1 ml to yield 0.01%) for cobalamin assay of diluted sea water. Assays are inoculated with one drop of depletion cultures grown in culture tubes for 3–6 days (thiamine, room temperature) and 7–10 days (cobalamin, 15°C) in media to which these vitamins were not added. Standard curves for each vitamin assay are performed simultaneously.

In collecting samples and acquiring other sorts of information about the Sound, we were governed by the following considerations. The concentrations of thiamine and cobalamin present at any given time will obviously be a resultant of production, transport, use, and destruction. If we assume that the production of cobalamin (Burkholder 1959, Starr *et al.* 1957) and probably of thiamine is due primarily to microbial activity, any variable affecting microbial synthesis—temperature, turbidity, depth, available nutrients—is likely to affect in turn vitamin concentration. The bacterial count, furthermore, might be expected to show some correlation with vitamin concentration. If these vitamins are produced mainly in the relatively nutrient rich areas—land, swamps, bottom mud (Burkholder and Burkholder 1956a, 1956b, 1958; Starr 1956)— and transported to the uper euphotic layers of water one would expect to find concentrations falling off away from these areas and varying with the volume of inflow or the stability of the water column. The amount of cobalamin consumed by auxotrophic microorganisms may be expected to vary seasonally with chlorophyll *a* content of the area sampled, since the major component of our early spring bloom is a cobalamin auxotroph, *Skeletonema costatum*. Vitamin concentration might also vary with zooplankton displacement volume, and with the populations of other types of auxotrophic microorganisms present. Non-biological destruction of cobalamin might vary with incident sunlight (Kashiwada *et al.* 1959) and that of thiamine with pH and temperature.

Beginning on 5 March 1958, surface samples were taken from Station 1 (41°11′N, 73°2′W), Station 3 (41°6′N, 73°0′W), and Station 5A (41°3′N, 72°59′W) at the same time as samples for the usual hydrographic data (temperature, salinity, turbidity, O_2, NO_3-N, PO_4-P, chlorophyll *a*, and plankton hauls) were obtained. Surface samples were taken in a plastic bucket, samples at greater depth with a Fjarlie bottle. The assay samples were immediately filtered through Whatman #42 paper and later through millipore HA or AA filters, and frozen with dry ice. The samples were stored in a dry ice chest until used. Hutner's volatile preservative was added on collection or before thawing. When it became apparent that surface samples from these three stations varied little on any one date, collections were made only at Station 5A but at 1, 2.5, 5, 10, 20, and approximately 40 m as well as at the surface. Later collections also included two series taken starting inside the breakwater of the Indian River at two or more depths. Counts of the bacterial population have so far been taken on one occasion only. Incident sunlight was estimated as described by Riley (1956). Only samples taken after 24 November 1958 were assayed for thiamine.

RESULTS

Seasonal variation of cobalamin in surface samples is plotted in Figure 2 together with temperature, and chlorophyll *a*, and in Figure 3 with NO_3-N and PO_4-P. It is immediately obvious that each of these factors shows some correlation with cobalamin concentration. As water temperature rose between 17 April 1958 (after the spring bloom) and 27 August 1958, cobalamin con-

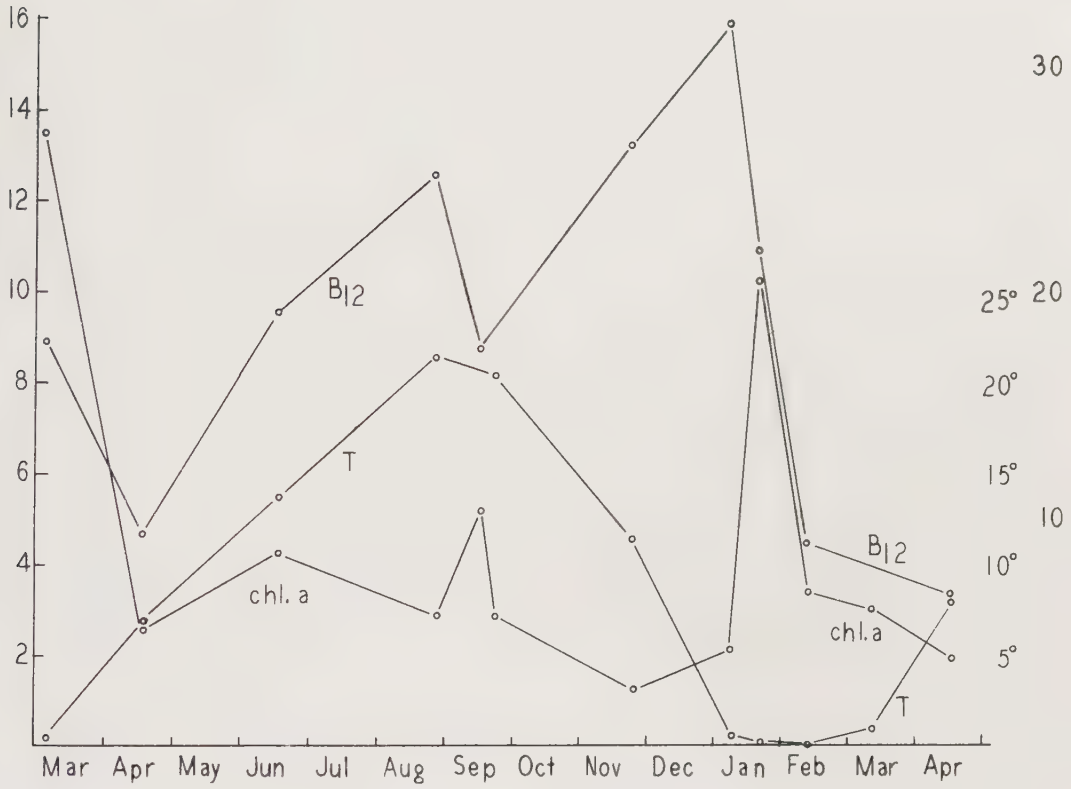

FIG. 2. B_{12} in Long Island Sound, averages of surface samples. Scale on right $\mu\mu$g/ml B_{12}; scales on left temperature and μg/L chlorophyll *a*.

tent gradually rose from 4.5 $\mu\mu$g/ml to 14.6–11.4 $\mu\mu$g/ml. The chlorophyll *a* content remained relatively stable during this period. With or after each spring bloom the cobalamin level fell. In 1958 it dropped from 8.8–9.1 $\mu\mu$g/ml in the earliest samples which contained 12–27 μg/L chlorophyll *a* to 3.9–5.2 $\mu\mu$g/ml on 17 April. In 1959 it fell from an average of 16 $\mu\mu$g/ml on 8 January in samples containing 2.7–4.5 μg/L chlorophyll *a*, through about 11 $\mu\mu$g/ml at the peak of bloom on 21 January, in samples containing 16.5–20.6 μg/L chlorophyll *a*, to 3.4 $\mu\mu$g/ml on 16 April. A similar effect was noted in the fall bloom of 1958. At Station 1 between 27 August and 17 September, cobalamin dropped from 14.6 $\mu\mu$g/ml to 8.8 $\mu\mu$g/ml while chlorophyll *a* rose from 1.9–4.5 μg/L to 10.4 μg/L.

PO_4-P and NO_3-N appear to reflect the requirements of phytoplankton growth as does cobalamin. It can be seen that, while all show minima at the same time with the decline of the late winter bloom, cobalamin concentrations more nearly parallel those of PO_4-P than of NO_3-N. It is presumed that the latter is limiting to phytoplankton growth in the spring and summer months. Distance from shore, depth (during the season of poorest vertical stability), salinity, O_2, PO_4-P, turbidity, and incident sunlight were not obviously correlated with cobalamin concentration. Insufficient data are available as yet on the effects of bacterial and zooplankton populations and of depth during the season of greatest vertical stability. It is quite probable, however that the high concentrations of cobalamin (up to 16 $\mu\mu$g/ml) attained over the winter are the result of turbulence, carrying up cobalamin from the rich bottom mud.

Thiamine presents a very different picture, since rarely could more than a barely detectable concentration (0–20 $\mu\mu$g/ml) be

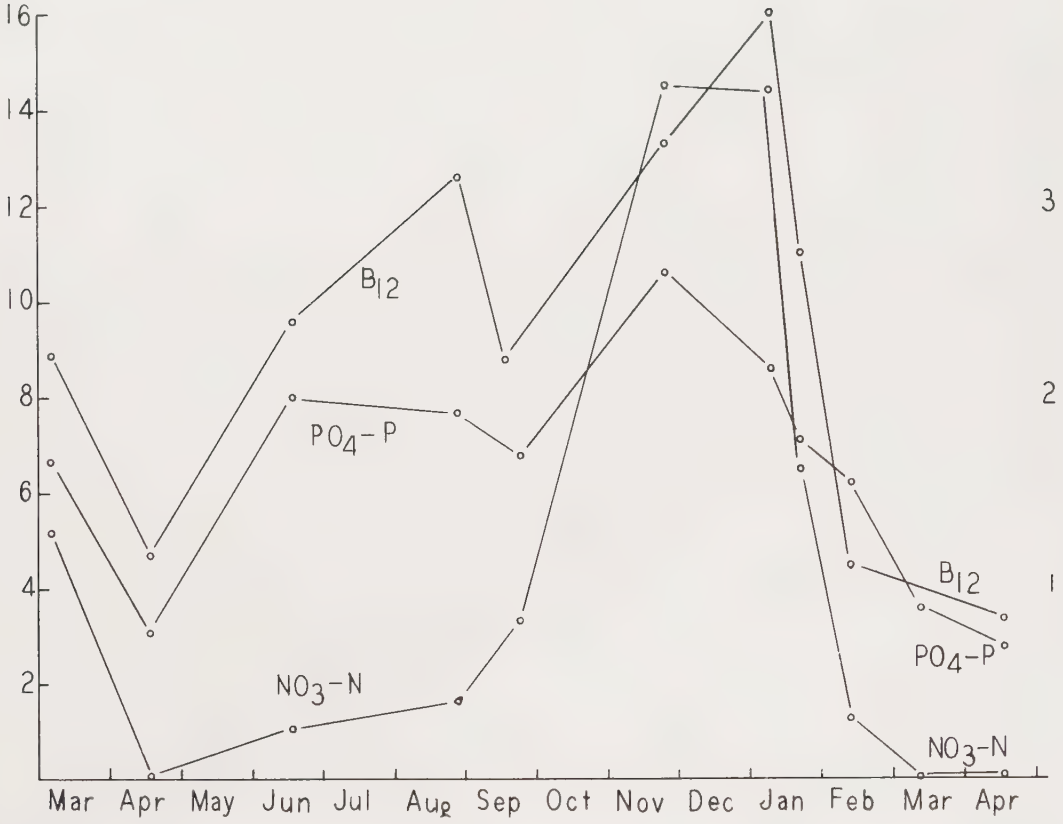

FIG. 3. B_{12} in Long Island Sound, averages of surface samples. Scale on right $\mu\mu$g/ml B_{12} and μg-atoms/L NO_3-N. Scale on right μg-atoms/L PO_4-P.

found in the body of the Sound. Samples taken in November on the way out to the routine stations showed 63 and 65 $\mu\mu$g/ml at the surface and at 3 m respectively within the breakwater of the Indian River and 40 and 30 $\mu\mu$g/ml at the surface and at 3 m at Charles Island. The decline in the concentrations at the surface as one moves offshore (Fig. 4) suggests that thiamine is derived from land drainage (in striking contrast to cobalamin in the Sound), and/or that thiamine produced in more saline water is destroyed faster under the more alkaline conditions. A second set of such samples, taken in April at high tide, contained almost no thiamine.

It seems reasonable to conclude, in spite of the paucity of data on cobalamin requirements under natural conditions, that cobalamin is never a limiting factor in Long Island Sound. The area is rich in cobalamin compared to the more open waters sampled by others. It supports a considerable seasonal population of the cobalamin auxotroph, *Skeletonema costatum*; as many as 12,470,000 cells/L were found in the spring

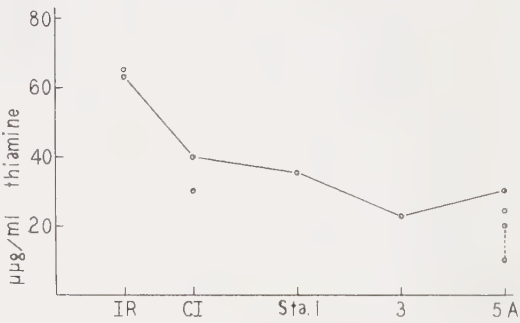

FIG. 4. Thiamine in Long Island Sound 24 November 1958. Solid line connects surface samples. Samples from Indian River, off Charles Island, Stations 1, 3, and 5A.

of 1958. The relative scarcity of thiamine and the absence of any of the few known thiamine auxotrophs from the local phytoplankton do not suggest a similar conclusion. Droop (1958) has found that thiamine auxotrophy is rarer among littoral isolates than cobalamin auxotrophy, although thiamine is perhaps the growth factor most frequently required by fresh-water and terrestrial microorganisms. The pattern of thiamine distribution also suggests that osmotrophic organisms requiring this vitamin will be rare in littoral areas and absent in oceanic waters. One presumes that for all the ease with which geneticists obtain auxotrophic mutants, these hereditary biosynthetic disabilities can become fixed in the genome of the species only when the ready availability of the growth factor throughout the habitat guarantees absence of negative selection pressure. The temptation to prophesy that vitamins will never be important limiting factors in marine ecology can be resisted by keeping in mind that habitats have been known to change and that populations have been known to invade new habitats.

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THE EFFECT OF TWEEN 80 ON THE ENUMERATION OF MARINE BACTERIA BY THE SPREAD AND POUR PLATE METHODS[1, 2]

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ABSTRACT

The effect of adding Tween 80 to water from Fisher's Island Sound was studied. Spread and pour platings, using media with and without yeast extract, showed highest counts by the spread technique, corroborating previous work. Tween 80 at 20 ppm was inhibitory; at 10 ppm showed only irregular increases, in contradiction to the findings with California waters.

INTRODUCTION

Studies of the role of bacteria in the economy of the sea practically always require enumeration. Many studies of procedural details have emphasized such requirements as appropriate temperature, gaseous environment, depth of culture medium in plates, concentration of nutriment, technique of inoculation. Uniform conclusions and recommendations are not always the result of these works. On the basis of higher total aerobic counts of mesophilic marine bacteria, Buck and Cleverdon (1960) proposed the spread plate as a method for their enumeration. Jones and Jannasch (1959) found that addition of surface active agents (including "Tween 80"[3]) to sea water samples prior to making pour plates gave increased counts, and that yeast extract was stimulatory to the growth of marine bacteria, corroborating the work of Carlucci and Pramer (1957). The present investigation concerned the effect of the addition of Tween 80 to water samples upon counts obtained by the pour and spread plating methods, using media with and without yeast extract.

METHODS

Surface samples were collected from July to December, 1959, in Latimer Reef, off the coast of Connecticut and east of Fisher's Island, New York. Sea water dilution blanks were autoclave-sterilized; pipettes (1.1-ml milk pipettes) were oven-sterilized. The plating media, those used by Reuzer (1933) and Carlucci and Pramer (1957), were of the composition shown in Table 1. Spread and pour platings and counts were made as previously described (Buck and Cleverdon 1960). Plates were incubated at 25°C. The Tween 80 was lot #478. An aliquot of a sterile aqueous solution was, when required, added to a sample to give the desired concentration. The sample was then hand-shaken prior to plating.

RESULTS AND DISCUSSION

Table 2 shows the superiority of a plating medium containing yeast extract in accordance with the findings of Jones and Jannasch and Carlucci and Pramer. Ratios of counts obtained on the medium of Carlucci and Pramer against those obtained on the medium of Reuzer were always larger (range 1.7–7.3; average 3.2). Tween 80 at 20 ppm

TABLE 1. *Composition of plating media employed*

Ingredients	Reuzer g/L	Carlucci-Pramer g/L
Peptone (Gelysate-BBL)	1.0	5.0
Yeast extract (BBL)	–	0.1
Glucose	1.0	–
K_2HPO_4	0.05	–
$FePO_4$	–	0.1
Agar (BBL)	15.0	15.0
Sea water: Salinity 30‰ pH	7.4–7.6	7.4–7.6

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[2] Contribution No. 4 from the Marine Research Laboratory, University of Connecticut, Noank, Connecticut.

[3] Atlas Powder Company, Wilmington, Delaware; brand of polyoxyethylene sorbitan monooleate.

TABLE 2. *Comparison of colony counts obtained by spread plates on media of Reuzer* (R) *and of Carlucci-Pramer* (C-P) *with samples untreated and with Tween 80 added*

Sample No.	Date and Tide	Colony counts × 10^2 No Tween		Ratios C-P/R	Colony counts × 10^2 Tween 80 (20 ppm)		Ratios C-P/R	Ratios of counts	
		R	C-P		R	C-P		C-P Tween/ C-P no Tween	R Tween R no T
1	7/10 Flood	26	55	2.1	23	81	3.5	1.5	0.89
2	7/17 Ebb	12	21	1.8	2.4	10	4.2	0.48	0.50
3	7/23 High	4.9	13	2.7	0.5	7.7	15	0.59	0.10
4	7/28 Flood	180	400	2.2	36	230	6.4	0.52	0.20
		Average ratios		2.2			7.3	0.77	0.42
				Tween 80 (10 ppm)					
5	7/30 Low	200	190	0.95	150	160	1.1	0.84	0.75
6	8/7 Flood	32	62	1.9	49	45	0.9	0.72	1.5
7	8/11 Low	100	150	1.5	120	150	1.3	1.0	1.2
8	8/18 High	6.5	16	2.5	6.5	16	2.5	1.0	1.0
9	8/20 Flood	31	40	1.3	20	46	2.3	1.2	0.65
10	8/24 Flood	49	89	1.8	51	91	1.8	1.0	1.0
		Average ratios		1.7			1.7	0.96	1.0

Average ratio of C-P/R under all conditions: 3.2. Average ratio of C-P Tween/C-P no Tween: 0.87. Average ratio of R Tween/R no Tween: 0.71.

was decidedly inhibitory on both media (average ratios 0.77 and 0.42), which accords with the data of Jones and Jannasch. Tween 80 at 10 ppm did not, however, produce a uniform increase in counts, contrary to the findings of Jones and Jannasch. With both media used, the counts were practically the same with or without the lower concentration of Tween 80 (average ratios 0.96 and 1.0).

Table 3 shows the apparent superiority of spread plates over pour plates (average ratios under all conditions 4.2), corroborating our previous study. Yeast extract in the

TABLE 3. *Comparison of colony counts obtained by spread and pour plates utilizing media of Reuzer* (R) *and of Carlucci-Pramer* (C-P) *with samples untreated and with 10 ppm Tween 80 added.* S = *spread plates;* P = *pour plates*

Sample No.	Date and Tide	Colony counts ×10^3 Tween 80 (10 ppm)				Ratio of counts (Tween 80)				Colony counts ×10^3 No Tween				Ratio of counts No Tween				Ratio of counts Tween 80/ No Tween			
		C-P		R		C-P	R	S	P	C-P		R		C-P	R	S	P	S	S	P	P
		S	P	S	P	S/P	S/P	C-P /R	C-P /R	S	P	S	P	S/P	S/P	C-P /R	C-P /R	C-P	R	C-P	R
1	10/27 Ebb	180	175	169	132	1.0	1.3	1.1	1.3	173	172	194	97	1.0	2.0	0.89	1.8	1.0	0.87	1.0	1.4
2	11/3 High	65	10	45	2.4	6.5	19	1.4	4.2	76	14	60	4.3	5.4	14	1.3	3.3	0.86	0.75	0.71	0.56
3	11/10 Flood	65	74	85	56	0.88	1.5	0.77	1.3	84	81	81	76	1.0	1.1	1.0	1.1	0.77	1.1	0.91	0.74
4	11/12 Ebb	3.2	2.6	2.3	1.4	1.2	1.6	1.4	1.9	4.7	2.8	3.8	2.4	1.7	1.6	1.2	1.2	0.68	0.60	0.93	0.58
5	11/24 Low	133	19	60	24	7.0	2.5	2.2	0.79	131	17	128	31	7.7	4.1	1.0	0.55	1.0	0.47	1.1	0.78
6	12/1 Ebb	3.8	1.0	2.4	0.46	3.8	5.2	1.6	2.2	4.1	1.7	4.2	0.50	2.4	8.4	1.0	3.4	0.93	0.57	0.59	0.92
	Average ratios					3.4	5.2	1.4	1.9					3.2	5.2	1.1	1.9	0.87	0.73	0.87	0.83

Average ratio of S/P under all conditions: 4.2. Average ratio of C-P/R under all conditions: 1.6. Average ratio of Tween 80/no Tween under all conditions: 0.82.

agar increases counts in almost all cases. Comparison between untreated and treated samples shows a slight inhibitory effect of Tween 80 in both spread and pour plates with both media regardless of whether average or individual ratios are considered.

The disparity of findings of the effects of Tween 80 on plate counts in the present study and in that of Jones and Jannasch may be due to differences in susceptibility to Tween 80 of the predominant bacterial floras of the two areas at the time of sampling or to limits imposed by numbers of samples, or to distinct differences in shaking procedure. ZoBell (1946) postulated the low concentration of nutrient material in the sea as being a factor in the clumping of marine forms, and it is thought that the variance between the two waters sampled emphasizes the need for additional chemical and physical studies of a variety of sea waters in conjunction with counts.

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PHYTOPLANKTON AND CHLOROPHYLL IN THE GERLACHE AND BRANSFIELD STRAITS OF ANTARCTICA[1]

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ABSTRACT

Studies were made on the phytoplankton and chlorophyll *a* content of waters in the Gerlache and Bransfield Straits of Antarctica during December 1958 and January 1959. Rich communities of diatoms, such as *Thalassiosira, Coscinodiscus, Eucampia,* and *Synedra,* and the chrysophycean *Phaeocystis* were observed at numerous stations in the Gerlache Strait and the western part of Bransfield Strait. Dinoflagellates were very scarce in this region. Antibiotic activity of the plankton was associated with *Phaeocystis.* The eastern area of Bransfield Strait, near the tip of the Antarctic Peninsula, was almost devoid of phytoplankton at all depths. Chlorophyll *a* determinations agreed in general with observations on the abundance of phytoplankton. Chlorophyll *a* ranged up to about 27 mg/m^3 of water, and the amount of pigment in surface waters was inversely related to total depth of the water.

INTRODUCTION

During the Antarctic summer of 1958–59, an opportunity was offered for studies on phytoplankton productivity in the marine waters along the western coast of the Antarctic Peninsula. Although our main effort was directed toward the verification and extension of observations on the antibiotic properties of phytoplankton (Sieburth 1959; Sieburth and Burkholder 1959), it seemed worth while to devote some attention to the distribution of phytoplankton communities and the chlorophyll *a* content of the plant plankton in the region indicated. In view of the dependence of Antarctic birds and fishes upon the photosynthetic plankton, it is important to gain some detailed knowledge concerning the seasonal, geographic and vertical distribution of the plankton and the factors that regulate primary production.

As an index of the potential photosynthetic capacity of the plankton, it was decided to determine the quantitative occurrence of chlorophyll *a.* Because of the limited time available for this work, only about 50 stations were studied, mainly in the region between the South Shetland Islands and the Antarctic Peninsula.

Earlier studies of the phytoplankton in the southern ocean have been devoted chiefly to floristic aspects that were of special interest to the various expeditions, such as the *Challenger* Expedition, the Voyage of the *Belgica,* Discovery Expeditions, etc. Valuable observations on the species of phytoplankton have been recorded during recent campaigns of the Argentine Naval Hydrographic Service (Frenguelli and Orlando 1958), but few results have yet appeared in available publications. In an extensive treatise on phytoplankton periodicity in Antarctic surface waters, Hart (1942) has pointed out how the plant plankton is almost entirely diatomaceous in the southern ocean that occupies more than 12 million square miles. Hart expressed the relative abundance of phytoplankton, taken in net hauls from 100 m to the surface, in terms of chlorophyll units, and showed that the more important species of diatoms had a completely circumpolar distribution in the oceanic belt extending around the Antarctic continent. The circumpolar distribution of plankton species was emphasized in a paper by Baker (1954). Among the earliest treatises on Antarctic

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diatoms were that of Castracane (1886) and the taxonomic paper of Van Heurck (1909), who studied the collections made on the Voyage of the S. Y. *Belgica* in 1897–99. Various papers on the distribution of species in samples collected by different expeditions were published by Heiden and Kolbe (1928), Hart (1934, 1937), Hardy and Gunther (1935), Hardy (1936), Hendey (1937), and Boden (1949). In contrast with the emphasis placed by Baker (1954) upon the general distribution of oceanic diatoms, Hardy (1936) published observations on the unequal quantitative distribution of oceanic plankton as a result of work with a continuous plankton recorder. Distribution of zooplankton in the Antarctic has been described by Mackintosh (1937), Foxton (1957), and others.

Greatly needed are continuous observations of plankton, pigment indices and the various factors that control primary production in the Antarctic. A few chemical values of Antarctic waters have been determined by Clowes (1938). In general, investigations on physical oceanography and meteorology have taken precedence over biology and chemistry on the Antarctic continent and in its surrounding waters. It is hoped that life studies there will soon receive the greater attention they deserve.

Surface ocean currents in the region of the Antarctic Peninsula flow easterly out of the Bellingshausen and Weddell Seas under the influence of prevailing western winds, and move steadily toward the southern tip of Africa. Preliminary observations indicate that the physical and chemical properties of the waters flowing through the Gerlache Strait may differ greatly from the waters of the Weddell Sea and the eastern part of Bransfield Strait. Large icebergs of continental origin float in the Bransfield Strait, sometimes called Mar de la Flota. In the Weddell Sea region southeast of Hope Bay, even in the summertime, solid ice fields and pack ice are very common. In contrast, the winter ice breaks up earlier in the Gerlache Strait, and life seemed to quicken in its waters during December and January of 1958 and 1959. The breaking of pack ice in this area was approximately two months later than in the summer of 1957–58. It is possible that the observations reported in this paper may indicate conditions at the beginning of the bloom period rather than the peak that frequently takes place in January. The distribution of phytoplankton was more generalized in late February, when rich blooms occurred in areas that were previously sparse, such as Deception Harbour and off King George Island. It seems worth while to report our data obtained for the distribution of phytoplankton, chlorophyll *a* and temperature at about 50 stations, in the hope that much further research will follow. A few samples were collected on the voyage of the icebreaker ARH *San Martin* from Buenos Aires to Deception Island, but most of our work was performed on the Hydrographic -ship *Chiriguano*, which operated mainly as a maintenance ship for Argentine lighthouses in the Gerlache and Bransfield Straits. The excellent cooperation of the captain, Capitán de Corbeta Carlos Mayer, his officers and crew, is gratefully acknowledged.

METHODS

At each station in the Antarctic, the surface temperature was recorded by direct reading of a Centigrade thermometer. Samples of plankton for microscopic examinations were obtained by towing Nos. 2, 12, and 20 nets. Other samples to be used for quantitative estimates of pigments were obtained by using a bucket at the surface, and Knudsen reversing bottles (See Barnes 1959) for other depths down to 150 m. Samples of plankton were examined under the microscope immediately and a portion of each was preserved by addition of neutralized formalin. Measured volumes of water, usually one liter, were filtered through Millipore filter pads to obtain samples of plankton suitable for the estimation of pigments. This method avoids some of the errors associated with procuring samples by use of nets, especially in waters where gelatinous algae are abundant. Hart (1942) attempted to avoid the errors introduced by clogged nets, through the use of 15-ml centrifuge tubes,

TABLE 1. *Relative abundance of genera observed in the microplankton. The numbers are estimated percentages in each community; T signifies a trace.*

Organisms	Stations																										
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	41	42	43	44	45	46	47	48	49	50	51	53
Biddulphia				10	T																5	5	5			5		T	30
Chaetoceros	T	30		20			15					T	10	T	5	T	T		T		5	T	5			5		5	T
Corethron	30	10		T	T	T				5		10	10	T		T	T	T	T		T	T	5						
Coscinosira					10		10																						
Coscinodiscus	T	15		T	10	20		80	15	5	10	5		5	15	T	5	5	15	T	10	5	10	85	T	25	50		T
Dinoflagellata			T								T			T														
Eucampia	5		10	15	20	T	5	T	5	5	10	T	25	T	5	5	5	30	25	10	15	10	10		T	20	20	5	30
Fragilaria	5			T		T	T		T	5	5		T	T	T	T		T	T		T	T		15	T	10	T	T	T
Melosira						5					T																		
Nitzschia		5			10					T							T						T					T	
Phaeocystis			30	30	20	70	60	5	50	60	30	75	10	85	15	80	70	40	25	85	35	45	35		40	25	10	80	10
Rhizosolenia	10			10	10	T	T		T	T	5	T	T	T	T	T	T	T	T		T	T			T	T		T	T
Silicoflagellata	T		T			T																							
Synedra	20	30	25	T	30	T	5	5	10	20	25	5	10	5	50	10	20	15	40	5	20	20	10			5	10	5	T
Thalassiosira	20		20	10	T	5	T	10	15		T	5	25		10	5					10	10	20		60	T	10	5	30
Tintinnoid										T	T	T			T			T	T									

but such samples are too small. In our work, the methods of Richards with Thompson (1952) and Creitz and Richards (1955) were followed. A small amount of $MgCO_3$ was added to the water at the time of filtration to preserve the pigments. The dried filter pads with plankton were stored in the presence of indicator desiccant (Drierite) in screw cap bottles, kept away from light and under refrigeration until extractions could be made at the end of the campaign. The pigments were extracted in 90% acetone and their absorption was measured in a DU Beckman spectrophotometer. Possible significance of chlorophyll data may be envisioned by consulting the paper of Ryther and Yentsch (1957), who review the literature and show how productivity may be calculated from pigment and light data.

RESULTS

Microscopic examination of the plant plankton revealed three main types of communities. One of these was a diatom population, with *Synedra reinboldii* and *Eucampia antarctica* very common constituent species. Such communities were often seen in the Gerlache Strait and the western part of Bransfield Strait. Another striking type of microplankton community consisted chiefly of centric diatoms, including species of *Coscinodiscus* and *Thalassiosira.* A third and very different community was dominated by the gelatinous globules of *Phaeocystis.* This type of plankton was caught as yellow-green slime on the tow nets and could be removed in large amounts with a spoon. *Phaeocystis* was associated with antibacterial activity, clearly evidenced in Petri plate tests with *Staphylococcus aureus*, *Mycobacterium smegmatis*, and other indicator bacteria (Sieburth and Burkholder 1959).

A list of the genera observed in the various samples is given in Table 1. Estimates of relative abundance of the different genera are stated in per cent figures, arrived at by educated guesses based upon microscopic

TABLE 2. *Chlorophyll a in mg/m³ and temperature of surface waters at different stations whose positions are indicated*

Date	Station No.	Temperature C°	Chlorophyll *a*	Latitude S	Longitude W
22 Dec. 1958	La Plata	+24.0	15.9	35° 22.5	56° 19.0
22 Dec. 1958	5	+22.5	11.1	36° 02.4	56° 22.5
22 Dec. 1958	6	+22.2	5.1	36° 37.0	56° 29.0
22 Dec. 1958	7	+22.0	0.4	38° 02.0	57° 02.0
22 Dec. 1958	8	+17.5	0.3	38° 51.5	57° 02.0
23 Dec. 1958	9	+12.5	1.1	41° 25.0	57° 11.5
23 Dec. 1958	10	+13.8	0.7	44° 11.8	57° 00.0
24 Dec. 1958	11	+12.2	—	47° 00.0	57° 00.0
24 Dec. 1958	12	+ 9.8	0.9	49° 45.0	57° 00.0
25 Dec. 1958	13	+ 9.0	0.5	52° 14.0	57° 22.0
25 Dec. 1958	14	+ 8.0	0.6	54° 00.5	57° 22.0
25 Dec. 1958	15	+ 7.0	—	55° 03.5	57° 22.0
26 Dec. 1958	16	+ 2.5	0.2	57° 45.0	57° 22.0
26 Dec. 1958	17	+ 2.0	0.3	60° 32.0	57° 22.0
2 Jan. 1959	19	− 0.2	5.8	62° 46.0	59° 49.5
3 Jan. 1959	20	− 0.6	12.9	63° 28.1	60° 52.0
3 Jan. 1959	21	− 0.4	17.3	64° 05.0	61° 08.0
3 Jan. 1959	22	+ 0.4	9.5	64° 16.2	61° 40.7
3 Jan. 1959	23	+ 0.5	7.7	64° 28.5	62° 17.5
3 Jan. 1959	24	+ 0.4	26.8	64° 43.5	62° 59.0
4 Jan. 1959	25	+ 0.5	—	64° 52.0	62° 54.0
4 Jan. 1959	26	+ 1.3	17.8	64° 37.8	62° 48.0
5 Jan. 1959	27	+ 0.4	1.7	63° 57.0	60° 49.0
5 Jan. 1959	28	+ 1.1	13.3	63° 38.5	60° 25.1
9 Jan. 1959	29	− 0.4	—	62° 41.0	60° 42.2
11 Jan. 1959	30	− 0.6	—	62° 35.0	59° 49.0
11 Jan. 1959	31	+ 0.5	—	62° 42.0	59° 38.0
14 Jan. 1959	32	− 0.2	14.2	62° 57.0	60° 39.0
14 Jan. 1959	33	+ 0.4	6.6	63° 00.0	59° 59.0
14 Jan. 1959	34	+ 0.4	2.1	63° 0.00	59° 10.0
14 Jan. 1959	35	− 0.4	0.4	63° 01.0	58° 37.0
14 Jan. 1959	36	− 0.4	—	63° 02.0	57° 58.5
15 Jan. 1959	37	− 0.7	0.3	63° 06.0	57° 07.0
15 Jan. 1959	38	− 0.9	0.4	63° 20.0	56° 57.0
15 Jan. 1959	39	− 0.8	0.5	63° 22.0	56° 58.0
15 Jan. 1959	40	− 0.9	0.3	63° 03.0	57° 23.0
16 Jan. 1959	41	− 0.6	13.9	63° 20.0	59° 46.0
16 Jan. 1959	42	+ 0.2	10.5	63° 32.0	59° 56.0
16 Jan. 1959	43	+ 0.4	13.0	63° 43.5	61° 05.0
16 Jan. 1959	44	+ 1.2	—	64° 11.0	61° 27.0
16 Jan. 1959	45	+ 0.7	—	64° 23.3	61° 50.0
17 Jan. 1959	46	+ 0.1	—	64° 31.0	62° 20.0
17 Jan. 1959	47	+ 0.6	8.0	64° 47.0	63° 07.0
17 Jan. 1959	48	+ 0.2	10.0	64° 52.0	63° 39.5
18 Jan. 1959	50	+ 1.3	5.3	64° 34.0	62° 39.0
19 Jan. 1959	51	+ 2.0	6.6	64° 25.9	62° 58.0
20 Jan. 1959	52	+ 0.9	11.3	64° 03.8	61° 28.3
21 Jan. 1959	53	+ 0.9	—	64° 29.0	62° 16.0
25 Jan. 1959	56	+ 0.6	6.2	62° 40.0	59° 25.0

observations. The locations of the stations are given in Table 2, along with temperature data and estimates of chlorophyll *a*.

Assistance in identifications of the various species of phytoplankton was kindly given by Dr. Paul S. Conger and Dr. Mary Parke. A list of species with brief comments is presented herewith.

Biddulphia striata Karsten was fairly abundant at Stations 21 and 53, and sparsely

distributed at some other places. *Biddulphia aurita* var. *obtusa* (Kütz) Hust. and an unidentified species of the genus were uncommon. *Chaetoceros tortissimum* Gran and *C. debile* Cl. were frequent species. Other representatives were *C. contortum* Schütt, *C. dichaeta* Ehr., *C. polygonus* Schütt, and the colonial *C. socialis* Lauder. *Cocconeis gaussii* Heid. and Kolbe occurred at a few stations. Several phases of the variable *Corethron criophilum* Castracane were often seen. *Coscinodiscus bouvet* Karsten sometimes contributed to the brown coloration of the water, as at Stations 25 and 47. *Coscinodiscus fasciculatus* O'Meara, *C. nitidulus* Grun. *C. oculus-iridis* Ehr., *C. radiatus* Ehr. and several unidentified species occurred occasionally. *Dactyliosolen antarcticus* Castracane was infrequent. A very common and variable member of the plankton was *Eucampia antarctica* (Castr.) Mangin. *Fragilaria antarctica* Castr. and *F. oceanica* Cl. occurred sparsely. Chains of *Melosira sol* Ehr. and *M. sphaerica* Karst. were observed at Stations 23 and 28. Species of *Pleurosigma* and *Nitzschia seriata* Cl. were uncommon.

Rhizosolenia alata Brightwell was often represented by several phases, but *R. hebetata* Bailey was infrequently seen. *Spinigera lanceolata* Heid. and Kolbe was identified tentatively. A very conspicuous and frequent species was *Synedra reinboldii* H. Van Heurck. At many stations, chains of *Thalassiosira gravida* Cl., *T. decipiens* Jörgensen, and *T. antarctica* Comber were abundant, with *T. condensata* Cl. sparsely represented.

The Antarctic phytoplankton in the region studied was almost entirely diatomaceous, except for *Phaeocystis* which occurred abundantly in some places. Our observations are in general agreement with those of Hart (1934, 1942), who found an abundance of diatoms in the Gerlache Strait and a relative paucity in old Bellingshausen water that drifts eastward through Bransfield Strait. However, the statement by Hart (1934) that in December more diatoms were observed at the tip of the "Palmer Peninsula" than in the Gerlache Strait is at variance with all of our studies made in 1959. Because of its productivity and antibiotic activity, *Phaeocystis* is a very important plankton organism in the Gerlache and western Bransfield Straits as well as in the Weddell Sea (Sieburth 1959). This organism occurred as cell aggregates held together in gelatinous masses of globular or irregular shape, and attaining a colony size up to about 1.5 mm across. The characteristics of this organism appear to agree closely with the description of *P. pouchetii* (Hariot) Lagerheim (1896) (See also Kornmann 1955). Hart (1942) apparently refers to this organism under the name of *Phaeocystis brucei.*

In the waters around the Antarctic Peninsula, dinoflagellates were observed rarely. In the oceanic phytoplankton of south temperate stations located approximately in the area of 36° S and 56° W, dinoflagellates were mixed with diatoms. Species of dinoflagellates were identified as follows: *Ceratium concavicornis*, *Ceratium fusus*, *Ceratium lineatum*, *Ceratium tripos*, *Dinophysis acuminata*, and *Peridinium antarcticum.* The communities of temperate plankton included also genera of diatoms as follows: *Coscinodiscus*, *Chaetoceros*, *Thalassionema*, and *Rhizosolenia*, although these were not as abundant as in the diatomaceous plankton of the Gerlache Strait.

The data presented in Figure 1 show very unequal values for chlorophyll *a* in the waters adjacent to the Antarctic Peninsula. The occurrence of greater populations of diatoms and yellow-green algae in the Gerlache Strait as compared with the eastern end of Bransfield Strait is paralleled by similar differences in chlorophyll *a* content of these waters. In northeastern Bransfield Strait, the values for chlorophyll *a* ranged from only 0.3 to 0.5 mg/m^3, whereas in the Gerlache Strait the values were commonly in the range of 10 to 25 mg/m^3. It is of interest that the highest chlorophyll *a* values observed in the Gerlache Strait are approximately equal to the chlorophyll *a* in the maximum blooms of plankton in Long Island Sound (Conover 1956) and possibly approach the theoretical maximum postulated by Gessner (1949). Our values appre-

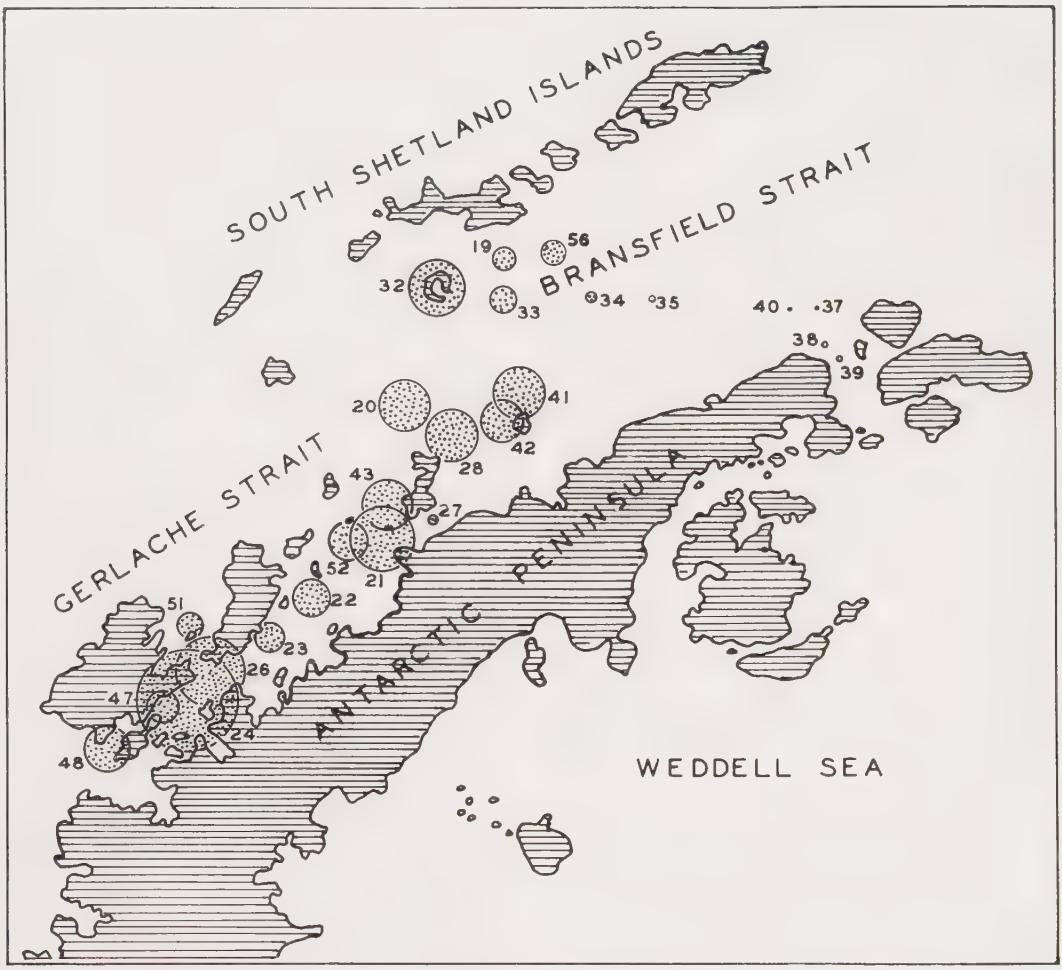

FIG. 1. The Gerlache and Bransfield Straits region showing location of certain stations and the distribution of chlorophyll *a*. The sizes of the circles are proportionate to the quantity of chlorophyll *a*; exact values are given in Table 2.

ciably exceed those given by Apollonio (1959) for the Arctic with a maximum of 0.37 mg/m^3 and those by Graham for phytoplankton at La Jolla, California, where the annual range was from 0 to 1.7 mg/m^3. Our data agree well with the data for the more productive regions mentioned by Ryther and Yentsch (1957).

Differences in water temperature seem not to explain the great variations in plankton content, because at any given temperature there may be much or little plankton. It would appear likely that light is an important factor in regions where the ice breaks up early and drifts in an easterly direction, leaving the waters open to the penetration of sunlight. Possibly the waters of the Gerlache Strait may be richer in essential nutrients, as a result of wind and tidal currents that cause upwelling and enrichment. Adequate studies of phosphate and nitrate along with other physical and chemical measurements would, doubtless, throw light upon the variations in geographical distribution of phytoplankton in these Antarctic waters.

Observations on the vertical distribution of chlorophyll *a* at 5 different stations are presented in Table 3. At all stations, the greatest concentration of pigment occurred

TABLE 3. *The vertical distribution of chlorophyll a in the marine plankton*

Station	Depth of Station fathoms	Depth of Sample meters	Chlorophyll *a* mg/m³
39	60	0	0.5
		10	0.4
		20	0.1
52	125	0	11.3
		10	11.8
		50	7.8
		100	5.3
26	250	0	17.8
		5	6.5
		10	8.4
		20	5.1
		50	4.4
		100	1.2
19	570	0	5.8
		7	5.0
		15	3.9
56	750	0	6.2
		5	3.8
		10	2.5
		20	2.9
		50	3.5
		100	2.9

at or near the surface. At Station 26, for example, the chlorophyll value was 17.8 mg/m³ at the surface and diminished steadily downward to 1.2 mg/m³ at a depth of 100 m. Examination of the pigment index in poor waters near Hope Bay also showed a decrease with increasing depth. It would be of great interest to determine the photosynthetic activity of this stratified plankton in relation to light intensity using methods similar to those of Ryther and Menzel (1959).

The poor development of phytoplankton in the eastern Bransfield Strait and waters of the Weddell Sea north of Robertson Island cannot be explained with the data now available. The puzzling feature was the presence of large penguin rookeries filled with fat young birds at Hope Bay. How were these birds obtaining adequate food supplies from the nearby sea waters so poor in phytoplankton? It is possible that the grazing euphausids were depressing the plant plankton.

On the voyage from Buenos Aires to the

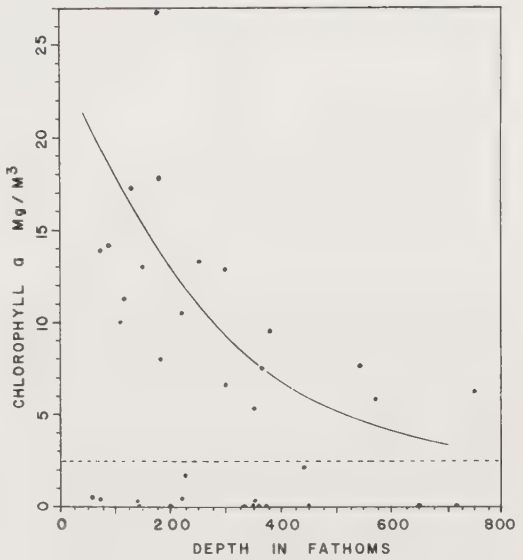

FIG. 2. The relation of chlorophyll *a* content of surface samples and depth of the waters shows an inverse correlation for values above 2.5 mg of chlorophyll *a* per cubic meter of water.

Antarctic, a few plankton and water samples were taken. The chlorophyll content of the estuarine waters in the region of La Plata was relatively high; a steady decrease was observed southward toward the Falkland Islands. A plankton tow, taken in the vicinity of the Falkland Islands, however, contained a rich population of centric diatoms and some dinoflagellates.

Thus, we have found relatively rich phytoplankton crops in estuarine regions, near islands, and in channels where increased levels of nutrients may be expected because of vertical mixing and some contributions from land areas. There appeared to be a definite relationship between "potential" productivity and water depth. The relation of chlorophyll *a* content of the surface water layer with water depth for Stations 19 through 56 is illustrated in Figure 2. Low values (below 2.5 mg/m³) were observed at various depths, perhaps because of the recent pack ice cover in some of these areas. However, for values above 2.5 mg/m³ there was a definite tendency for increasing amounts of chlorophyll *a* to be associated with decreasing depth of water. In the Gerlache region, regeneration of nutrients in the

shallower waters probably takes place through exchanges with bottom sediments and only to a small extent by glacial transport from the land.

In conclusion, it may be said that there is good evidence from our work, and from the investigations of others, that the phytoplankton is unevenly developed in different geographic areas of Antarctica. In some regions, such as the Gerlache Strait, standing crops of phytoplankton during the Antarctic summer compare favorably in amounts with crops that we have observed in temperate waters, such as Long Island Sound, or near the Georgia Sea Islands. The seasonal variations in Antarctic plankton deserve intensive study in relation to mechanisms of distribution in pack ice and by currents, and to the various ecological factors that regulate biological productivity. The present contribution represents so little accomplished in an area that has so much to offer.

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SURFACE SCHOOLING AND FEEDING BEHAVIOR IN THE WHITE BASS, *ROCCUS CHRYSOPS* (RAFINESQUE), IN LAKE MENDOTA[1]

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ABSTRACT

Zooplankters of the genus *Daphnia* comprise the bulk of the food of the white bass, *Roccus chrysops*, in Lake Mendota, Wisconsin. Compact schools of white bass are conspicuous at the surface from May through October. Planktonic *Daphnia* are highly aggregated, on a relatively small scale in foamlines or roll vortices, and on a larger scale by horizontal convergence on the leeward side of important shoal areas. The white bass are able to locate regions of high concentrations of air-locked and/or free-swimming *Daphnia*, as shown by highly significant differences between the mean numbers of organisms found within and outside of feeding areas. Suggestions are made as to the mechanisms involved. The relatively limited but significant vertical migration of *Daphnia* in Lake Mendota consists of typical morning and evening maxima at the surface. The pattern of feeding activity of the white bass is shown to correspond with the morning and evening concentrations of *Daphnia* in the surface waters. Some effects of the feeding behavior upon the efficiency of food-intake are discussed.

INTRODUCTION

Many aquatic animals show diel periodicity, which is correlated with rhythms in the physical environment or with interrelated biological rhythms. The white bass, *Roccus chrysops* (Rafinesque), with their intense and conspicuous schooling behavior visible at the surface, and the cladocerans of the genus *Daphnia*, with their readily measured vertical migrations, are particularly suited to studies of behavior patterns in the field.

In Lake Mendota, Wisconsin, the white bass is primarily a pelagic species. During the summer months 90% of captures by gillnet are within 6 m of the surface (Tibbles 1956). Comparatively compact schools of young-of-the-year and yearling fish are formed and show a high degree of stability. Riggs (1952) and others suggest that this schooling stability decreases with age, the older fish being in smaller schools. During the summer the schools are composed of both sexes. In Mendota, the common schooling associates of adult white bass are the yellow perch, *Perca flavescens* (Mitchill), and the crappie (*Pomoxis*); the northern spottail shiner, *Notropis h. hudsonius* (Clinton) is common in schools of yearling fish. The majority of schools are composed predominantly of white bass, with the associated species observed in very small numbers.

Most of the white bass, observed at the surface in Mendota during the summer months, are feeding upon *Daphnia schødleri* Sars, *D. galeata mendotae* Birge (*longispina*) and *D. retrocurva* Forbes, although a small segment of the population (age-group V and above) rely more on small fishes for food (Horrall 1956). This is in sharp contrast to the findings of Sigler (1949) on the white bass of Spirit Lake, Iowa, where they feed primarily on the young of panfish, although the very young take *Daphnia* in considerable volume.

Surface schooling of white bass occurs from May through October in Lake Mendota. In the early morning and late evening, and occasionally throughout the day, they are commonly observed in schools at the surface over bar regions ranging in depth from

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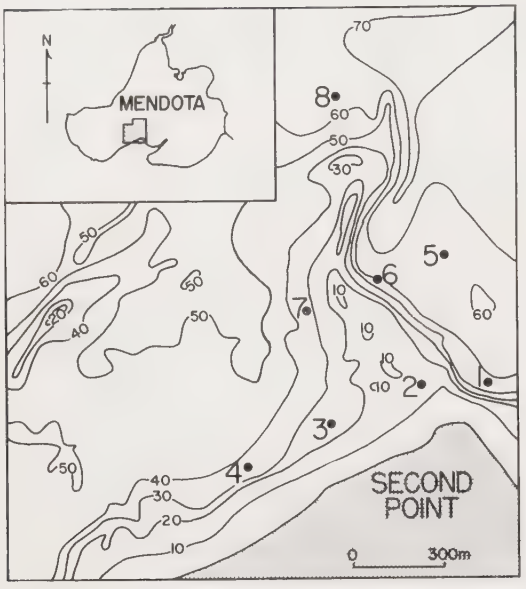

FIG. 1. Location of eight permanent stations on Second Point Bar, Lake Mendota. Contours for lake depth are given in feet.

3 to 15 m, such as Second Point Bar (Fig. 1). When foamlines are present, the fish invariably move up the foam track into the wind, whereas in calm weather, they mill about in apparent "frenzy" feeding, with no obvious compass bearing to the movement of the school. In these foamlines, *Daphnia* are concentrated and may become trapped in the surface film in sufficiently large numbers to be readily visible. *Daphnia* become "air-locked" when a bubble of air lodges within the carapace.

From observations both in the laboratory and the field, it appears that yearling white bass pick up individual *Daphnia* when feeding. The older fish (age-groups II–IV), however, make a subsurface sweep, some 20 to 40 cm in length, at a depth of 10 to 20 cm, with mouth agape and opercles spread. They then break through the surface film, causing the disturbance by which schools are readily sighted.

There were two objects of the program: 1) to determine if the white bass are able to locate areas of high concentrations of air-locked or free-swimming *Daphnia*, and thus feed with greater efficiency, and 2) to investigate the environmental factors involved in the surface schooling of white bass.

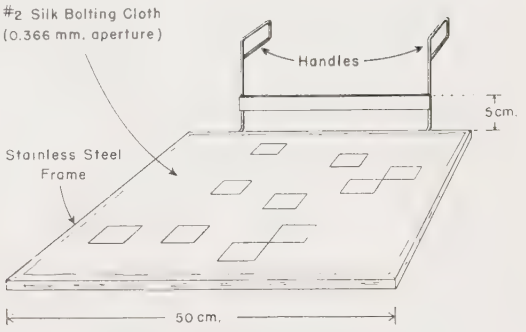

FIG. 2. Apparatus for the sampling of *Daphnia* air-locked at the surface.

SURFACE FEEDING AND SCHOOLING IN RELATION TO CONCENTRATIONS OF *DAPHNIA*

A sampling program was designed to measure the number of *Daphnia* trapped at the surface, as well as those free-swimming directly below. Eight permanent stations were located on Second Point Bar, Lake Mendota (Fig. 1). In addition, following a survey of the study area on each sampling cruise, a buoy was placed within each of two actively feeding schools of white bass. During every cruise, a 3-min plankton tow (approximately 900 L) was taken with the Clarke-Bumpus sampler at each of these 10 stations. The sampler was equipped with a net of #2 bolting silk and towed at a depth of 25 cm. Counts were made by the Sedgwick-Rafter method.

Also, an estimate of the numbers of surface air-locked *Daphnia* was made. The sampling apparatus comprised a piece of #2 silk bolting cloth stretched over a square stainless steel frame (Fig. 2). Ten randomly placed squares (5 cm × 5 cm) were drawn on the screen. It was dipped to a depth of about 5 cm, swung under an undisturbed surface directly forward of the bow of the boat and then lifted vertically. The *Daphnia* within each of the 10 squares were counted. The total number of *Daphnia* caught on each of the 10 squares during 45 lifts was found to be approximately equal (935.0 ± 70.5). There was therefore no evidence of

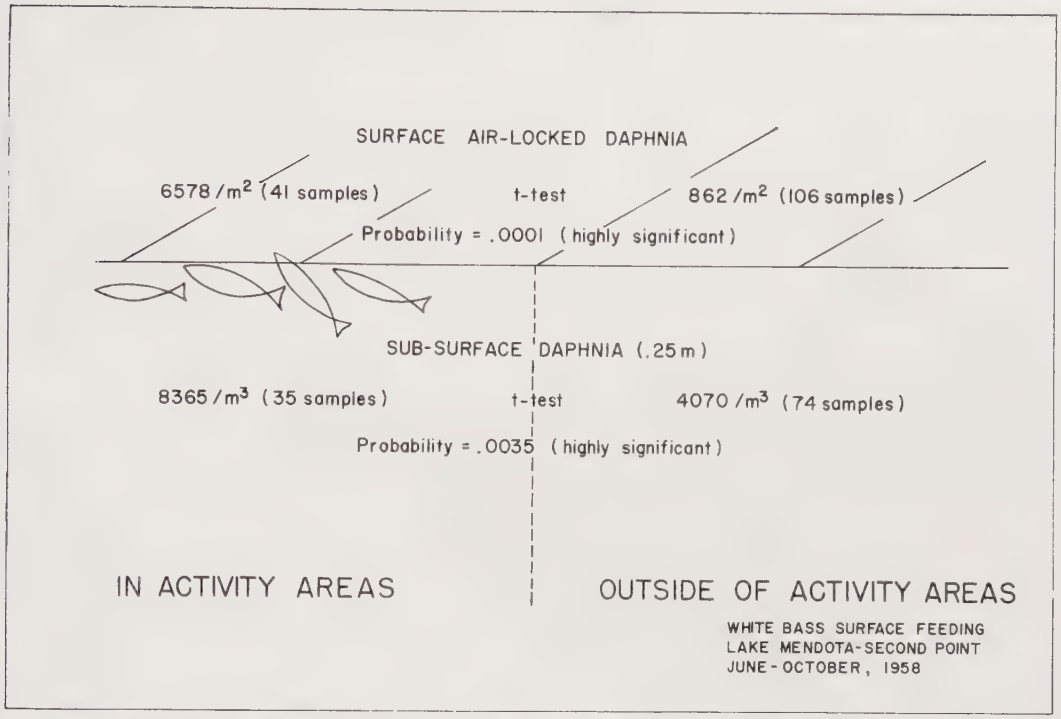

FIG. 3. Comparative numbers (mean) of air-locked and free-swimming *Daphnia*. Areas with white bass schooling activity contrasted to areas without activity.

organisms washing to the more central squares on the screen. All stations were sampled in random order, the average time for two boats to cover 10 stations being 42 min.

The planktonic organisms were highly aggregated. In the Second Point area there seem to be at least two physical factors to account for this. Relatively small scale variations in numbers of zooplankters occur because they are concentrated in the foamlines or roll vortices (Stommel 1949). On a larger scale, the horizontal convergence of currents aggregates the zooplankters on the leeward side of the bar (Clarke and Bryson 1959). Wind-induced convergence produces concentrations of *Daphnia* which drift about the lake, wherein the individuals maintain their depth in relation to light intensity (Ragotzkie and Bryson 1953). These aggregations may be transported to the Second Point area.

The data from the 1958 surface sampling program are shown in Figure 3. All cruises where 4 or more schools were sighted were included; less schooling activity was deemed inadequate for our purposes.

Such highly significant results indicate that the white bass are somehow able to seek out areas of high concentrations of air-locked *Daphnia* and/or free-swimming *Daphnia* which are concentrated just below the surface.

ENVIRONMENTAL FACTORS RELATED TO SURFACE SCHOOLING OF WHITE BASS

A series of 24-hr sampling programs was designed to determine the environmental factors involved in and related to the surface schooling of white bass. Horizontal tows of 3-min duration were taken with the Clarke-Bumpus sampler at depths of 0.25 m, 1 m, and 2 m at a single station. The location of the station was determined by a plot of the schooling activity from the previous summer, so as to place the station in an area of maximum likelihood of surface schooling. Customarily, 30 samples were taken at each of the three levels during each 24 hr cruise.

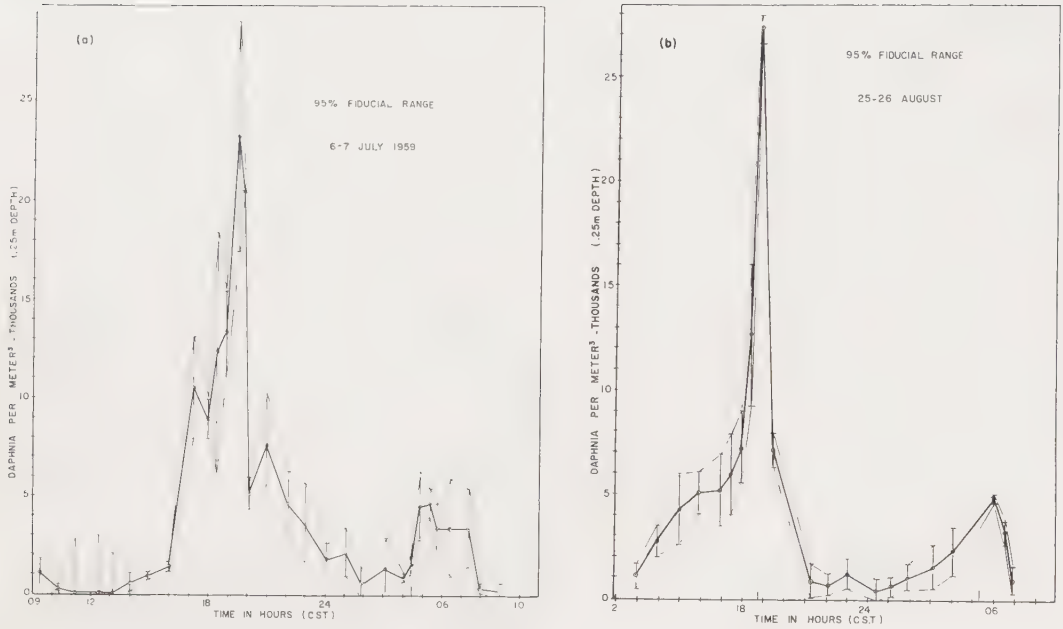

FIG. 4 (a–b) Numbers of *Daphnia* over 24-hr period (0.25 m). Fiducial ranges derived from counts of three 1-ml aliquots. (See Figs. 6a and 6d.)

Using the Sedgwick-Rafter method, three 1-ml aliquots were counted in entirety, and 95% fiducial ranges were derived from these data (Fig. 4a and 4b).

Transects were drawn between the 8 permanent stations (Fig. 1). This was done in an effort to eliminate bias in determining the surface schooling of white bass and to have a comprehensive record of white bass activity to compare with the migratory pattern of *Daphnia*. Six standard cruise patterns were designed; the first three covered each transect once, as did the second three. An observer on the designated cruises plotted all observed schools on the cruise sheet, in addition to the time at the start and finish of each cruise.

Light measurements were taken in the air and below the surface, at 10 cm, 1 m, and 2 m, with a Whitney underwater-light-meter (a Weston photronic cell calibrated in foot-candles). In the latter part of this study, a permanent-recording apparatus was available through cooperation with the Meteorology Department of the University of Wisconsin. Four photronic cells were mounted on a tower in the water at the designated depths and coupled with a recorder on shore.

The theories concerning the vertical migration of zooplankton organisms are well summarized by Cushing (1951), who considered light to be the most important single factor, with temperature, age of zooplankton, weather, and the density of phytoplankton also important. Juday (1904), using sampling techniques that were up to that time untested, believed that he had found a limited vertical migration of *Daphnia galeata* (*hyalina*) in Mendota, but none in the case of *D. pulex*. Worthington (1931) described the vertical movements of *D. longispina* and noted that morning and evening peaks of high surface concentration were characteristic of this species.

In Lake Mendota the vertical migration of *Daphnia* consists of the typical evening ascent to attain an evening peak at the surface, followed by a period of midnight sinking (Fig. 5). The morning maximum in Mendota is typically lower than the peak of the previous evening. The morning maximum is followed by the daytime low at the surface (Figs. 5 and 6).

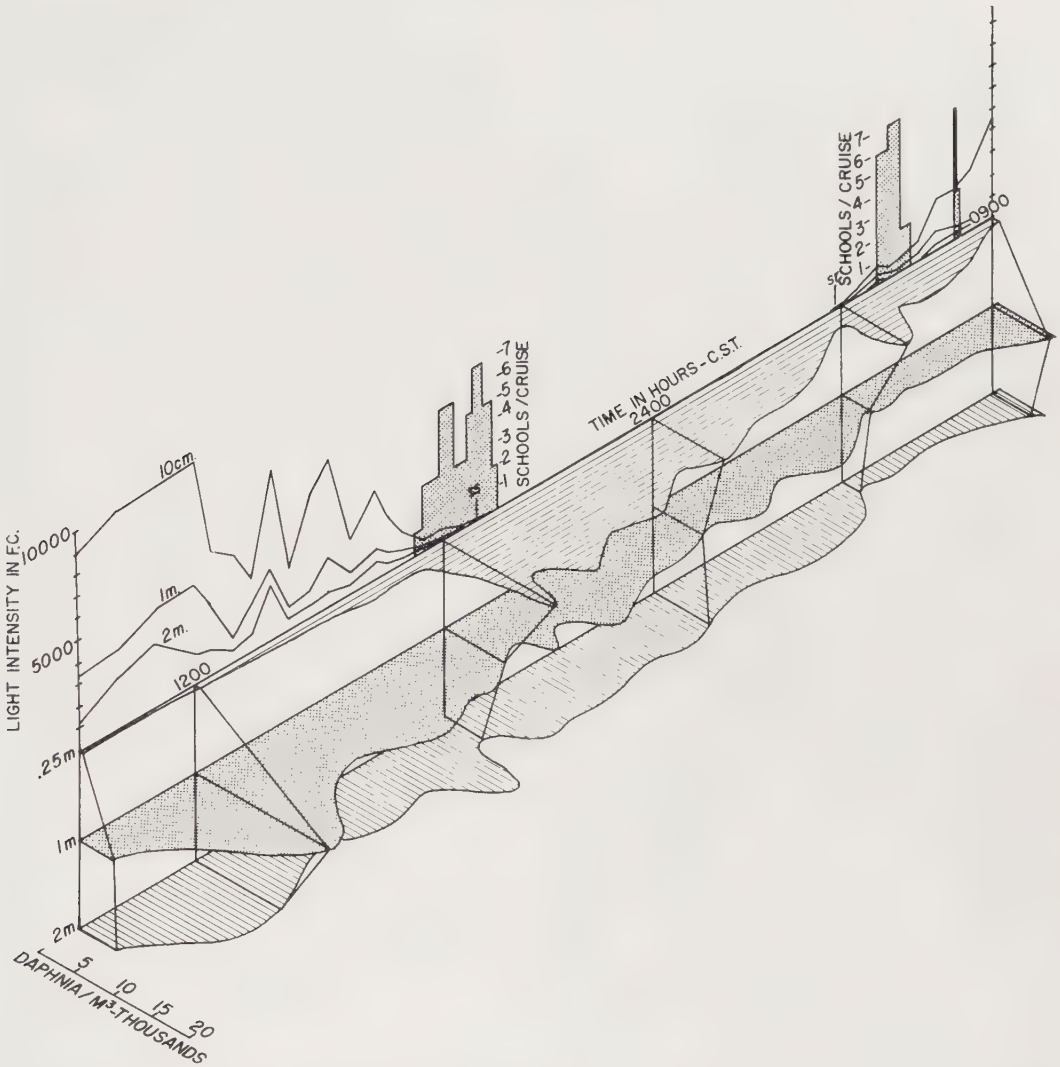

FIG. 5. Three-dimensional diagram of schooling activity and related environmental factors extending over 24 hr (horizontal axis) on July 27–28, 1959. Schooling activity of white bass (bar graph), numbers of *Daphnia* (0.25-m, 1-m, and 2-m depths) and light intensity (———) over a period of 24 hr. Each curve determined by 30 samples. sr = sunrise, ss = sunset.

The vertical movement is not great, only 1 m or less (Fig. 5), but the difference in numbers between the daytime low at the surface (0.25 m) and the evening and morning maxima of *Daphnia* is exceedingly great.

The feeding of the white bass at the surface, at dawn and dusk, is shown to be correlated with the surface maxima of *Daphnia* (Figs. 5 and 6), which are the principal food of the schooling white bass in Lake Mendota.

DISCUSSION

The question arises as to whether the white bass ascend to the surface in response to, 1) light intensity; 2) the vertical movement of the principal food organism (*Daphnia*), which in turn is known to respond to light intensity; or 3) a series of unknown and interrelated factors. The response of *Daphnia* to changing light intensity is well illustrated in Figure 6c. An abrupt decrease in

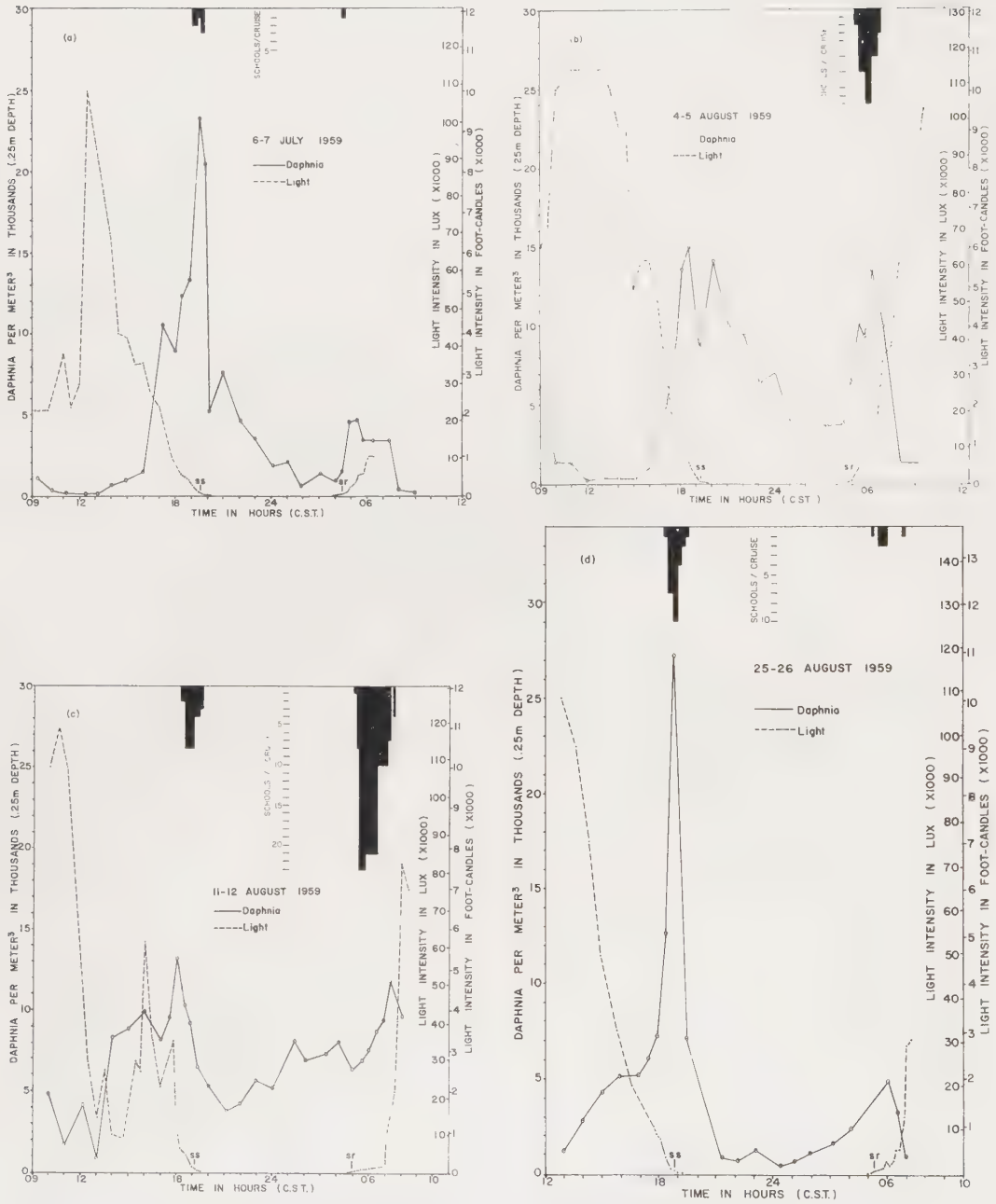

FIG. 6. (a–d) White bass activity and related environmental factors. Schooling activity (bar graph), numbers of *Daphnia* at 0.25-m depth (———), and light intensity (- - - - -) over four periods of approximately 24 hr. sr = sunrise, ss = sunset.

light intensity at 1200 hr apparently initiated the evening ascent to the surface somewhat earlier than might be expected, although the evening peak was attained at the normal time.

Steven (1959) believed that fish associate diel changes in light with vertical movements of food organisms. Admittedly beyond his evidence, he also suggested that fish may follow concentrations of substances

liberated by plankton in their diel vertical migrations and thus arrive at the surface with the plankton. Balls (1951) and Richardson (1952), using echo-sounding techniques, found that schools of herring (*Clupea harengus*) and sprat (*C. spattus*) rose to the surface at night and descended at daybreak. Richardson concluded that this movement was in direct response to light. Hasler and Bardach (1949) believed that light intensity, either acting directly or through its effects on food organisms, and the feeding stimuli as such, only partly explained the movement of perch in Lake Mendota. Hasler and Villemonte (1953) found that, during the summer and early fall, a rapidly changing light intensity set off the movement of perch to Second Point, where they rested on the bottom at night, but concluded that the orientation mechanism remained unexplained.

We have no evidence that the regulation of this pattern of morning-evening activity in the white bass is of an endogenous nature. We feel that the white bass may be able to locate dense concentrations of *Daphnia*, at some distance below the surface, and possibly follow aggregations in vertical movement by means of an acute sense of smell. In future work it may be of interest to study the development of interrelated behavior patterns of the white bass and *Daphnia*, and to consider these in relation to their evolutionary history. The material is at hand for this type of approach.

The data presented above indicate that the white bass are able to locate areas of high concentrations of both air-locked and/or free-swimming *Daphnia*. This, in general, is similar to the type of evidence summarized by Hardy (1956) and Lucas (1956) for herring (*C. harengus*) feeding upon *Calanus*. Whales are also able to locate areas where euphausiids are concentrated (Hardy, *op. cit.*). As Wunder (1936) explained long ago, plankton-eating fish place themselves in the water where they find their food in greatest concentration.

While surface feeding occurs in a variety of different patterns of zooplankton distribution, the situation whereby *Daphnia* are concentrated in a distinct foamline, up which white bass move in a characteristic pattern of behavior, is unique and predictable. Let us further analyze this one situation. From beneath the surface, a foamline appears to a man in an underwater observation chamber as an extensive white highway. A portion of the early morning light is both scattered and refracted in a general downward direction by the bubbles of foam. It is entirely possible that a combination of surface air-locked *Daphnia* and foam may act as a visual cue to surface feeding fish, thus enabling them to remain in the foam tract where the zooplankton is concentrated. Both the observed behavior of the white bass and the preceding data lend support to this hypothesis.

An examination of the ratio of air-locked to subsurface *Daphnia* indicates that these same air-locked *Daphnia* constitute an important fraction of the total food ingested. With a subsurface concentration of 8,300 *Daphnia* per m^3 and a corresponding surface aggregation of 6,500 air-locked *Daphnia* per m^2, consider the case of a white bass removing all free-swimming *Daphnia*, of a given size, from a cylindrical column of water 40 cm in length, terminating the run by breaking through the surface film. The fish would encounter approximately twice as many organisms as it breaks through the surface, as it would encounter in the subsurface cylinder. This assumes that the fish removes all comparable forms from a surface area equal to that of the base of this subsurface cylinder.

A white bass 305 mm long has a gape of approximately 7 cm^2. Under the above conditions, such a fish would encounter 6.9 *Daphnia* per sweep. If we assume that a fish makes a run every 10 sec, which is probably conservative, this would account for 2,484 *Daphnia* per hour of feeding. Stomachs examined during the morning period of activity, which may extend for 1 to 2 hr or more, commonly contain from 100 to 2500 *Daphnia*. Assuming a moderate efficiency in feeding, these values appear reasonable even though the rate of digestion is unknown. In addition, the fish may be able to locate con-

centrations undetected by our sampling techniques.

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INCIDENCE OF THE COD PARASITE *LERNAEOCERA BRANCHIALIS* L. IN THE NEW ENGLAND AREA, AND ITS POSSIBLE USE AS AN INDICATOR OF COD POPULATIONS

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ABSTRACT

A total of 4,519 cod, *Gadus morhua* L., from the coastal and offshore regions of New England were examined during June to December 1957 for the parasitic copepod, *Lernaeocera branchialis* L. Infestation decreased from north to south and inshore to offshore.

The effect of infestation on the length–weight relationship of cod was examined and found non-significant. An examination of infestation selectivity by fish size also showed no significant differences.

From the differential infestation rates, it is shown that four general groups of cod can be distinguished: those of the northern Gulf of Maine heavily infested, the moderately infested central and southern Gulf cod, the lightly infested Georges Bank population, and the southern New England group which is free of infestation. This supports previous unpublished tag return data, and indicates the usefulness of *Lernaeocera* for distinguishing various groups of cod.

INTRODUCTION

Investigators of the problem of group differences within fish species, employing methods such as meristic counts, age and growth comparisons, morphometric studies and tagging have been able to separate and identify some lesser divisions (Marr 1957). Serological studies (Cushing 1952), physiological determinations (Farris 1957) and uses of naturally occurring parasites as biological tags (Sindermann 1957; International North Pacific Fisheries Commission 1956) have also been utilized with varying degrees of success.

For several years, scientists of the Fisheries Research Board of Canada have been collecting data on the infestation of cod, *Gadus morhua* L., by the copepod parasite *Lernaeocera branchialis* L. Templeman (1953) reported differential infestation rates, low in the offshore region of Newfoundland and relatively high in the southeastern inshore area.

The purpose of the present study was to determine whether differential infestation rates also exist in New England waters. An attempt was made to determine the effect of infestation upon the condition of the fish and to establish a relationship between the size of cod and infestation rate. A limited amount of pertinent life history data concerning *Lernaeocera* was also collected.

The area chosen for study includes most of the New England coastal region and adjoining offshore banks, extending northward from Pt. Judith, Rhode Island, to the Islands of Campobello and Grand Manan, New Brunswick. This area had previously been divided into statistical subareas by the North American Council on Fishery Investigations (Rounsefell 1948). These subareas were used as basic units of study, treating the fish taken from each of them independently (Fig. 1).

METHODS

From June until December 1957, a total of 4,519 cod were examined in the New England area for incidence of *Lernaeocera*.[1] Sampling was opportunistic because of the

[1] A. G. Humes of Boston University confirmed our identification of the parasite.

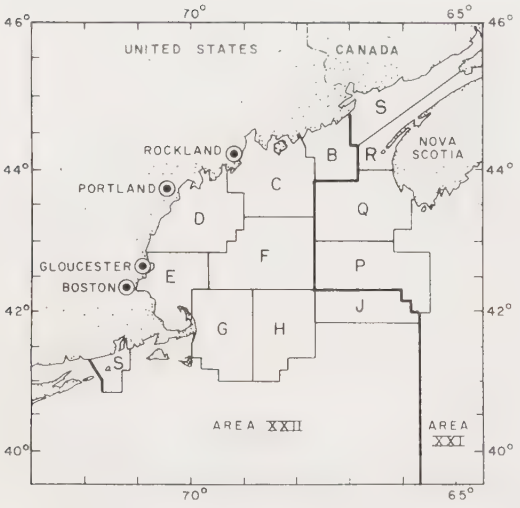

FIG. 1. Statistical subareas discussed in text (after Rounsefell, 1948).

normal vagaries of the fishery and the weather, but an attempt was made, wherever possible, to obtain samples from each of the various market size categories of cod landed and from the different fishing areas. Generally, these objectives were achieved with the exception of the largest size category. These were scarce in the commercial catch and when present, were usually beheaded, making it impossible to ascertain the presence or absence of the parasites.

The method of sampling varied slightly according to conditions but ideally all of the infested and non-infested cod were measured to the nearest millimeter (fork length) and weighed to the nearest ounce. Examination of cod for the presence of the adult parasite is simple due to the nature of the organism, which is large (ranging from 1.5 to 2.6 cm in length with the average about 2.3 cm) and blood-red. It may easily be seen attached to the isthmus of the gills when the fish is placed on its dorsal side with the opercles spread.

Most of the fish were examined at the dockside after they were unloaded from commercial vessels. The validity of this method was checked on one or two occasions by sampling the same vessel's catch at sea and in port. Sometimes softer body parts of the parasite were crushed, but this did not affect results since the elongated chitinous "neck" remained imbedded and could easily be detected either by visual examination or by running thumb and forefinger along the isthmus.

Circulars were sent to fish dealers and bait-shop operators in an effort to secure specimens of *Lernaeocera* from a wide variety of environments in New England. As a fortunate result, an immature "Pennella" stage not previously recorded from the Western Atlantic was found attached to a 32-cm cod caught south-southwest of Plymouth, Massachusetts, in 30 ft of water.

A. M. Fleming (personal communication) of the Fisheries Research Board of Canada has found larval stages on the gills of the lumpfish (*Cyclopterus lumpus*), indicating that in Canadian waters as in Europe this fish is an intermediate host. The gills of 30 lumpfish from various parts of the Gulf of Maine area were examined in the laboratory during the present investigation. Of these, 6 from the inshore Eastport area were infested with larval *Lernaeocera*.

RATES OF INFESTATION

Details of the life history of *L. branchialis* are to be found in Scott (1901), Sproston (1942), Capart (1947, 1948) and Dollfus (1953). It is probable that the adult female stays on the definitive host for a period of years. A survey of the literature indicates that it has a boreo-arctic distribution in the Atlantic which parallels the distribution of *Gadus* spp. in all areas excepting the southerly sections of the coastlines of Spain and the United States. In these areas, cod penetrate farther south than *Lernaeocera*, indicating some limiting factor for the latter. The distribution of some intermediate host(s) might be suggested as a possibility.

In the following discussion of the samples collected, notes explain the sampling conditions and peculiarities of the fishery in each subarea as they affect the samples. Fish sizes are defined as: Small, 0–50 cm; Medium, 51–75 cm; Large, 76–100 cm; and Extra Large, 101 cm and over. These correspond rather closely to the market categories used in some areas: Scrod, 1½ to 2½ lb;

Market, 2½ to 10 lb; Large, 10 to 25 lb; and Extra Large (sometimes called "Whales"), over 25 lb.

Eastern Maine—Subarea XXII B: All the fish examined were taken from the Grand Manan Banks area in depths ranging from 30 to 70 fathoms and were examined at sea during Cruise 105 of the *Albatross III*. Of 390 fish examined 26 (8.9%) were infested.

Central Maine—Subarea XXII C: The only cod readily available for sampling in this north central section of the Gulf were landed in Manset, Maine, by a small group of draggers operating in the nearby Blue Hill Bay region. Twenty-four cod were available; of these 7 (29.2%) were infested and two had bilaterally attached parasites.

Western Maine—Subarea XXII D: The cod sampled from this region were caught near shore along that segment of the 50-fathom isobath which extends 20 miles southward from Cape Elizabeth, Maine. A total of 413 cod were examined; of these 36 (8.7%) were infested.

Small cod were not represented. This can be attributed to gear selectivity: all of the cod examined were landed by gill netters operating from Portland, Maine. These fishermen utilize a large mesh which is highly selective for bigger fish.

Inner Grounds—Subarea XXII F: This central area of the Gulf showed an infestation rate of 7.6%, based on 25 infestations found on examination of 331 cod.

There were very few small fish. The reason for this is again gear selectivity. The most characteristic feature of this section of the Gulf is its rocky shoaling bottom, which makes dragging hazardous at best. Cod, however, are found here in large numbers. The only efficient gear for use in these waters is hook and line; the absence of small fish in the catch is explained by the use of the large hooks, baited to attract the larger, more profitable, fish.

Eastern Massachusetts—Subarea XXII E: The cod examined from this area were landed by two groups of vessels: sport fishing boats and small commercial draggers, both operating in relatively shallow inshore waters, to 30 fathoms. Of 685 cod examined 51, or 7.5%, were infested. The landings of the commercial catch were examined at the port of Boston while those of the sport fishing boats were sampled at various small ports along the Massachusetts coast, including Plymouth, Scituate, Cohasset, Hull, Rockport and Gloucester.

Sampling in this area was rather evenly distributed through the different size categories. Two additional non-size categories were added: 1) heads, from those fish of about medium size which had been beheaded, and 2) mixed, cod of all sizes with length measurements unobtainable as a result of the rapid processing at the fish plants in which these samples were taken.

West Side of the South Channel—Subarea XXII G: The Boston medium trawler fleet often fishes heavily in this nearby area during the summer months. As a result, it was possible to examine 1122 cod. Of these, only 9 or 0.8% were infested. The distribution of infestation was about the same through all size categories.

East Side of the South Channel—Subarea XXII H: The Boston medium trawler fleet which fishes this area, located approximately 100 nautical miles east of Provincetown, remains away from port from 5 to 7 days. Such an extended period at sea coupled with the warm weather and melting ice in the fish hold during summer increases the danger of bacterial decomposition. For this reason the gills of all fish exceeding scrod size (2½ lb) are removed. In order to secure samples of intact cod from this offshore area it was necessary to make a trip aboard a commercial vessel. Examination of 193 cod revealed only two *Lernaeocera* (1.0%).

Northern Edge and Northeast Peak of Georges Bank—Subarea XXII J: This section of Georges Bank is fished intensively by the Boston large trawler fleet. Although the catch of these vessels comprises the bulk of New England cod landings it was rather difficult to secure samples. All the fish landed from vessels which remain at sea for upwards of 10 days during the summer months must by law have the gills removed. A limited number of cod with gills intact were secured by placing large canvas sample bas-

kets (200-lb capacity) aboard a few of the vessels. These were filled by the fishermen and examined at dockside when the vessel returned to port. However, the greatest number of cod were observed during a 10-day trip aboard the trawler *Wisconsin* and during Cruise 104 of the *Albatross III*. A total of 767 cod were examined and of these 14 (1.8%) were infested.

Rhode Island Shore—Subarea XXII S: This area, lying off Point Judith, was the southernmost sampled. A total of 212 cod landed by vessels of the local industrial fish fleet were examined. None was found with *Lernaeocera*.

Western Browns Bank—Subarea XXI P: The observations in this area were made during Cruise 105 of the *Albatross III*. There was only one infested cod found during examinations of 82 individuals (1.2%). All of the fish examined were taken in the shoal area (30–65 fathoms).

Western Nova Scotia—Subarea XXI Q: This sample was also secured on Cruise 105 of the *Albatross III*. Eight cod were examined and one of these was infested with two *Lernaeocera*, bilaterally attached. The observations were made on cod taken from some 6 miles south of the Lurcher Shoal Lightship in depths of 30 to 45 fathoms.

Northern Bay of Fundy—Subarea XXI S: The only reasonably accessible places for sampling in this region were the islands of Campobello and Grand Manan, located at the mouth of the Bay of Fundy. Here the daily catches of many family-owned small hook and line vessels are landed.

A total of 292 cod landed at the ports of White Head and Seal Cove, Grand Manan and Wilsons Beach, Campobello were examined. Of these, 95 or 32.5% were found to be infested with one or more *Lernaeocera*.

INFESTATION SELECTIVITY

The percentage of infestation by size for all samples is shown in Table 1. A χ^2 value of 2.12 (2 d.f.) demonstrated that there were no significant differences in infestation rates among the small, medium and large fish. A comparison of the extra large category was not made because of the small sample in this size range.

TABLE 1. *Percentage of infestation by size category*

Size category	No. of fish	No. of infestations	% infested
Small	1,381	83	6.0
Medium	2,121	114	5.4
Large	487	27	5.5
Extra Large	57	1	1.7
Heads	156	22	14.1
Mixed	293	20	6.8
No measurement	24	0	—
Total	4,519	267	5.9

CONDITION OF INFESTED FISH

Previous investigations on the effect of *L. branchialis* on the definitive host have been carried out in European waters (Schuurmans-Stekhoven 1936; Mann 1952; Capart 1948; Sproston 1942; and Kabata 1958). All reach the general conclusion that *Lernaeocera* is harmful to the definitive host, but fail to agree as to the extent of damage. However, their work involved several gadoid species not found in North American waters.

In the present study the length–weight regressions for infested and non-infested fish are almost identical:

Non-infested cod, $\log \hat{y} = -4.381 + 2.829 \log x$

Infested cod, $\log \hat{y} = -4.543 + 2.915 \log x$

Where x = length in mm and y = weight of eviscerated fish in lb.

Neither the intercepts ($t = 1.3500$; d.f. = 89) nor the slopes ($t = 1.2818$; d.f. = 89) show significant differences. Superficially the infested cod appeared healthy; their flesh was firm and their skin coloration similar to that of non-infested fish. However, in the absence of age data, there is no evidence that their growth rate was normal.

There was no significant difference in infestation rates between various size categories of fish. It can be concluded, therefore, that the parasite does not select its definitive host by size or cause a differential death rate.

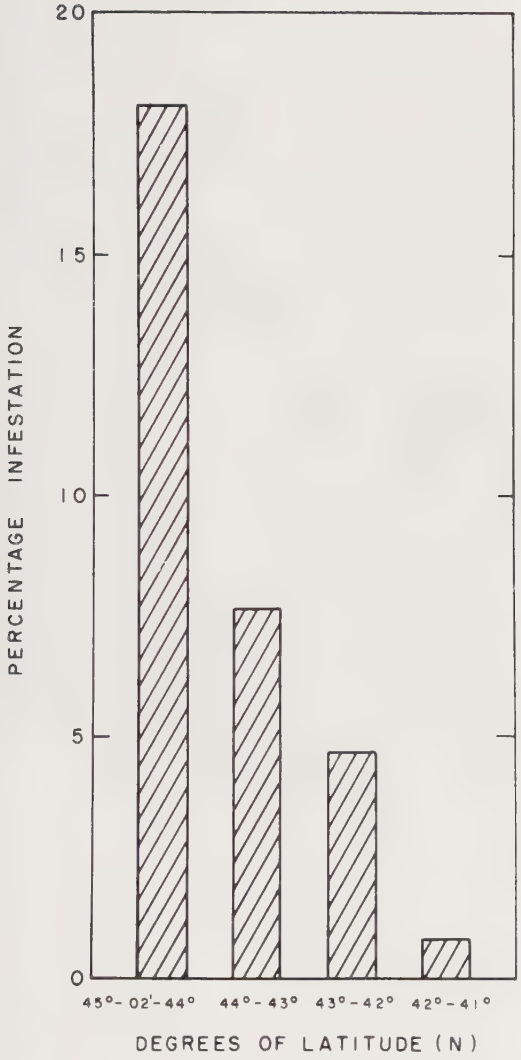

FIG. 2. Percentage infestation by latitude.

DISTRIBUTION OF INFESTATION

A differential occurrence of *Lernaeocera* on cod is present in New England waters. It is evident that the infestation rates assume a pattern of decreasing intensity from north to south in the region of investigation (Fig. 2). This fact, when considered with the Atlantic occurrence of the copepod, indicates that it is an organism of the boreo-arctic regions.

The vicinity of Cape Cod has long been recognized as the zone of transition between the boreal and temperate fauna. That this area would represent the southern limit in abundance of boreal species such as *Lernaeocera* or the lumpfish (*Cyclopterus lumpus*) is therefore not surprising. However, the cod extends its general range both south and west of Cape Cod in sufficient numbers during the winter months to support a fishery in the vicinity of Cape May, New Jersey (Wise 1958). In the present study this southern group of cod as represented by the XII S sample was found free of infestation while those to the north presented an increasing gradient of infestation northward.

Fish taken within 20 miles of the shore (13 to 40 fathoms) had an 8.3% infestation compared with 3.0% for those taken more than 20 miles from the coast. A similar gradient is characteristic of infestation of gadids by *Lernaeocera* in other areas. Templeman (1953) reported a similar situation in Newfoundland waters and Sproston and Hartley (1941) and Kabata (1957) in the coastal waters of Great Britain. Sproston (1942) concluded that infested fish do not migrate with the main stock, thereby increasing the inshore and estuarine infestation rates.

The inshore-offshore infestation pattern parallels the distribution of the intermediate host, the lumpfish, which according to Bigelow and Schroeder (1953) are restricted to a depth of a few fathoms in the Gulf of Maine. It would seem, therefore, that infestation will only occur in the shallow inshore waters of the Gulf when both the lumpfish and cod coincide there. The wide lateral distribution of the adult *Lernaeocera* may be explained by the movements of the cod, which are far less restricted (Bigelow and Schroeder 1953) than those of the lumpfish.

Sproston and Hartley (1941) estimated the minimum length of the gadid life cycle phase of *Lernaeocera* to be 8 weeks. They also found that no definite breeding period could be assigned because four or five consecutive generations were produced year-round, with a great degree of overlap. The percentages of infestation in the present study, although established only during the warmer months of the year, become more reliable as indicators of actual conditions

when supported by the results of Sproston and Hartley.

Bigelow (1927) described the dominant non-tidal circulation pattern in the Gulf of Maine as a general anticlockwise eddy. This, when considered with both the drift bottle data of Fish and Johnson (1937) and the drift pattern of the boreal pteropod *Limacina retroversa* (Redfield 1939), suggests that *Lernaeocera* will tend to be localized in the Gulf. The distance traversed by any individual larva would be negligible because of its limited (about 24 hr) planktonic existence. It is most likely that significant dispersal is accomplished during the time the larvae are attached to a host. If Bigelow and Schroeder (1953) are correct concerning the distribution of the lumpfish it becomes evident that all newly fertilized female copepods originate in shallow inshore waters. Because of their limited duration of planktonic life, they must encounter a definitive host in this area. Consequently, horizontal dispersal would be determined largely by the presence of cod during this critical time of *Lernaeocera* development.

The tagging experiments of Schroeder (1930) and Wise (1958) indicate a discrete self-contained population of cod in the area south of Nantucket Shoals. The results of the present investigation lend support to this conclusion. No infestation was found in the Middle Atlantic–Nantucket Shoals group sampled at Point Judith, Rhode Island, during the autumn migration. The light infestation found on Georges Bank and in the South Channel area indicate little mixing beween this group and those to the north and south. Moderate infestation in the central Gulf and heavy infestation of the northern coastal region suggests that mixing between these groups occurs regularly.

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RELATIONS BETWEEN PRIMARY PRODUCTION, CHLOROPHYLL AND PARTICULATE CARBON

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ABSTRACT

In two very different areas in the North Sea, Aberdeen Bay (7 m) and the Fladen Ground (140 m) seasonal cycles of C^{14} uptake, chlorophyll and particulate organic carbon were observed. The ratios of C^{14} uptake to chlorophyll concentration showed marked variations seasonally. There were no signs of "dead" chlorophyll or of a decrease in the ratio due to nutrient deficiency. The ratios of chlorophyll to particulate carbon suggest that in coastal waters living plants generally form the most important part of the particulate carbon. At the deeper position the ratio was much smaller so that chlorophyll is not a good index of organic matter in the water.

INTRODUCTION

Although chlorophyll concentration and C^{14} assimilation have been widely used as estimates of phytoplankton populations and their growth rates, much less is known about the relations between these measurements and the quantities of particulate organic matter in the sea. Gillbricht (1952), from a statistical analysis of chlorophyll, cell counts and "seston" measurements in Kiel Bay, deduced that only 4% of the organic matter was living and that there was about as much chlorophyll associated with detritus as there was in living plants. He calculated that for diatoms the chlorophyll to carbon ratio was 1:4, and for dinoflagellates 1:12. These large ratios have been criticized by Banse (1956). Riley (1959) and Riley and Harris (1956), from a comparison of millipore filtered and net samples in Long Island Sound, deduced very different values. During the spring outburst they estimated that 70% of the organic matter was living and during the remainder of the year, 37%. The probable range of chlorophyll to carbon in the plants varied from 1:30 to 1:100. Parsons and Strickland (1959) consider that the proportion of living plants in the organic matter is much higher inshore than offshore.

In the hope of gaining some insight into these problems, it was decided to combine C^{14} and chlorophyll measurements with estimates of particulate organic carbon determined by wet oxidation. Two contrasting regions in the North Sea were chosen for the observation of a year's cycle—the very shallow turbid waters in Aberdeen Bay and the comparatively clear and deeper (140 m) position on the Fladen Ground which has already been studied in some detail (Steele 1956).

METHODS

The particulate organic matter was filtered and estimated by the method described by Fox, Isaacs and Corcoran (1952). Filtration is through a pad composed of equal weights of SiO_2 (Hyflo Super-cel) and MgO. This acts by adsorption and can remove colloids such as molecular haemoglobin (Fox, Oppenheimer and Kitteridge 1953). The organic carbon is estimated by wet oxidation and titration. It was found necessary to wash the filter pad with 250 cc of distilled water to remove salts which affect the titration. The samples collected at sea were stored in a deep-freeze before analysis.

This method is comparatively simple and is not time consuming. The interpretation of the results as carbon may not be exactly true but the relative variations should be consistent. For the other factors measured, the methods employed are comparatively standard. The values for C^{14} uptake incorporate the isotope factor suggested by Steeman Nielson (1952) but no allowance is made for respiration. The chlorophyll values were obtained from 90% acetone extracts measured at 665 mμ on a Unicam SP 600 calibrated with pure chlorophyll *a*.

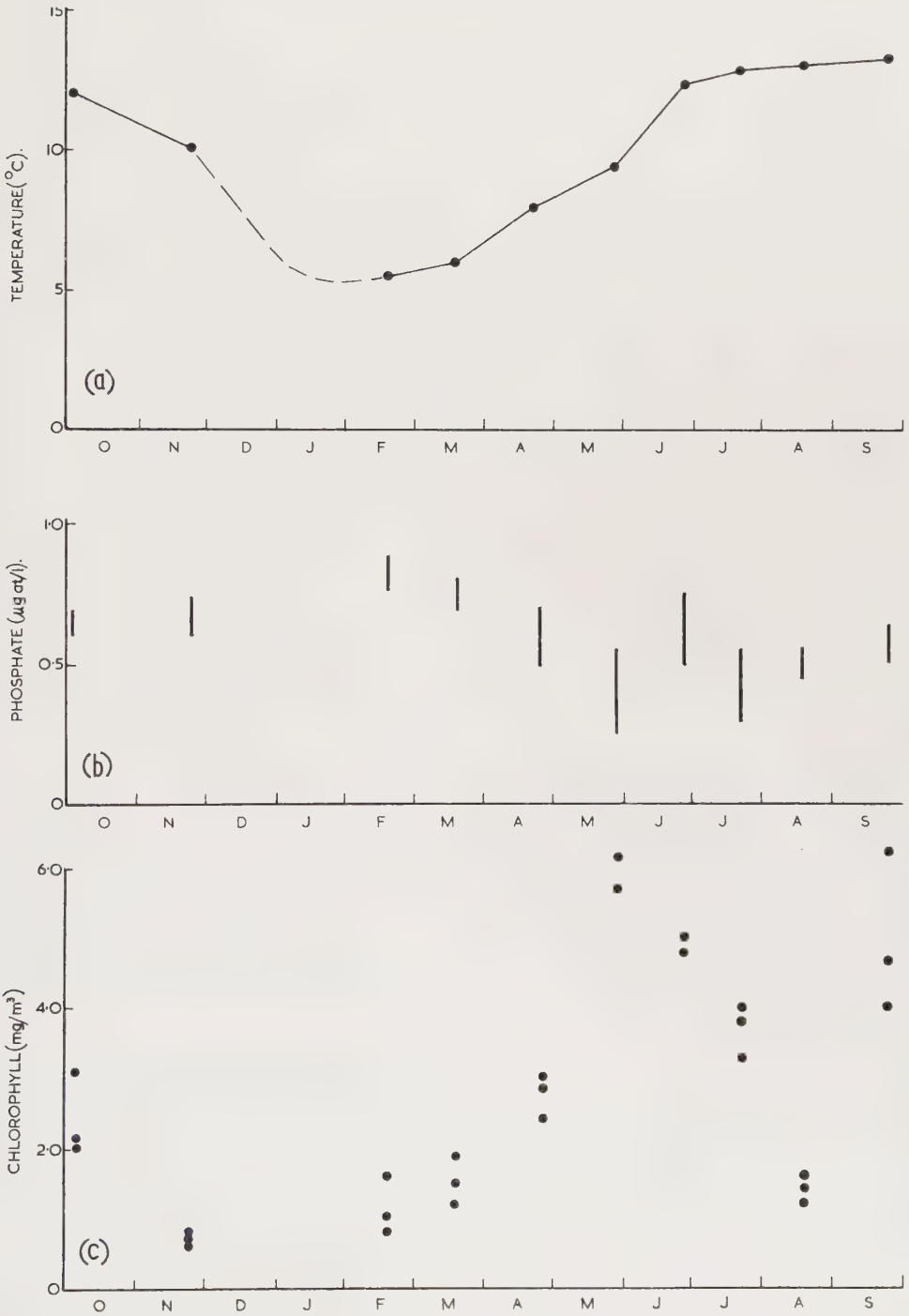


FIG. 1. Data from Aberdeen Bay, 1958–59. a) Mean temperature. b) The range of phosphate values. c) The average of the surface and bottom chlorophyll concentration for each day.

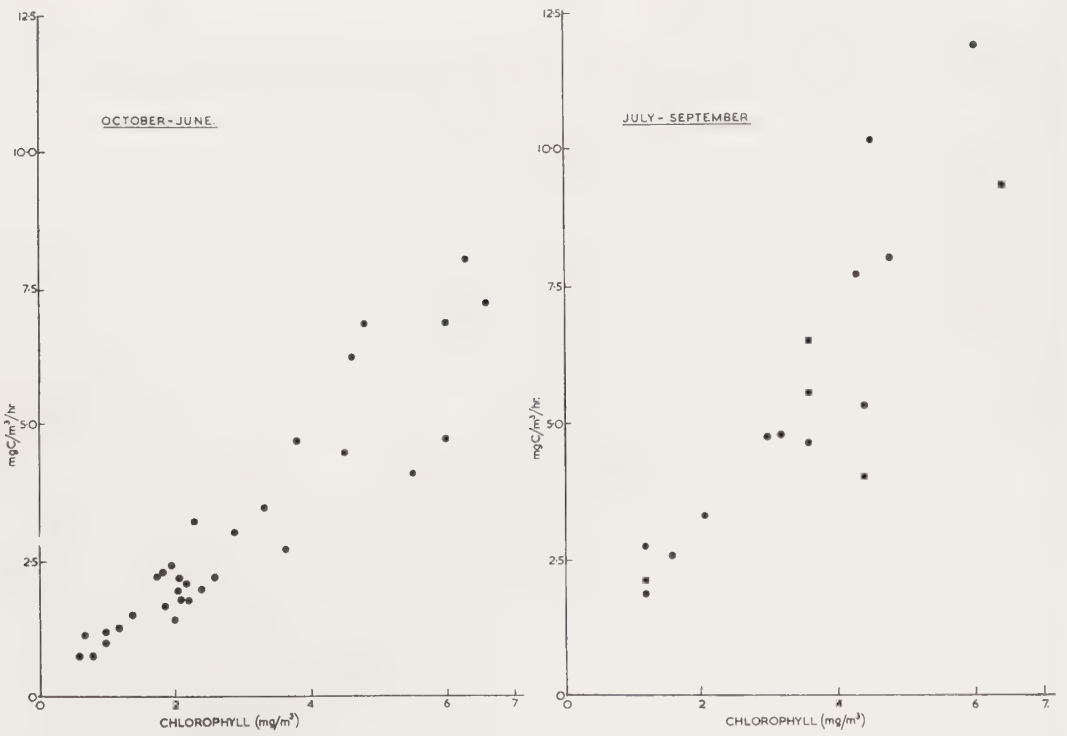


FIG. 2. Relations between carbon assimilation at 840 ft-c and chlorophyll concentration in Aberdeen Bay.

The water samples were collected with a perspex twin-sampler of the Van Dorn type (Van Dorn 1956) holding about 5 L. This enabled the chlorophyll, carbon and C^{14} measurements to be made from the same "dip."

Aberdeen Bay

Samples were collected at one position from October 1958 to September 1959, generally on three consecutive days each month. The water depth was usually 6 to 8 m, and temperature, salinity, phosphate, chlorophyll, C^{14} and particulate carbon were sampled from near surface and near bottom.

The salinity varied between 33.5 and 34.6‰ except for two rather lower values. Since the salinity in the main body of the North Sea is about 35.1‰, the mixture with fresh water run-off at this station was about 3% and so the water is, effectively, "marine." The Secchi Disc values varied between 2.5 m and 8.0 m with a mean value of 4.2 m. From March to September, samples for ashing were taken to determine the inorganic particulate matter. The surface samples generally lay between 0 to 5 g/m^3 whereas the near bottom values were mainly in the range 5 to 30 g/m^3. From this, and also from the texture of the samples, it was evident that the turbidity was caused by the suspension of particles from the sandy bottom of the bay.

Figure 1 gives the mean temperature, the range of phosphate values during each period of consecutive sampling and the average of the surface and bottom chlorophyll values for each day. The last of these shows that the day-to-day variations are much smaller than the changes between months so to some extent the values will represent seasonal changes.

The C^{14} samples were exposed for 4 hr at a light intensity of about 840 ft-c in a constant temperature room at 13°C. The relations between C^{14} uptake and chlorophyll values are given in Figure 2. They have been divided into two groups since there seems to

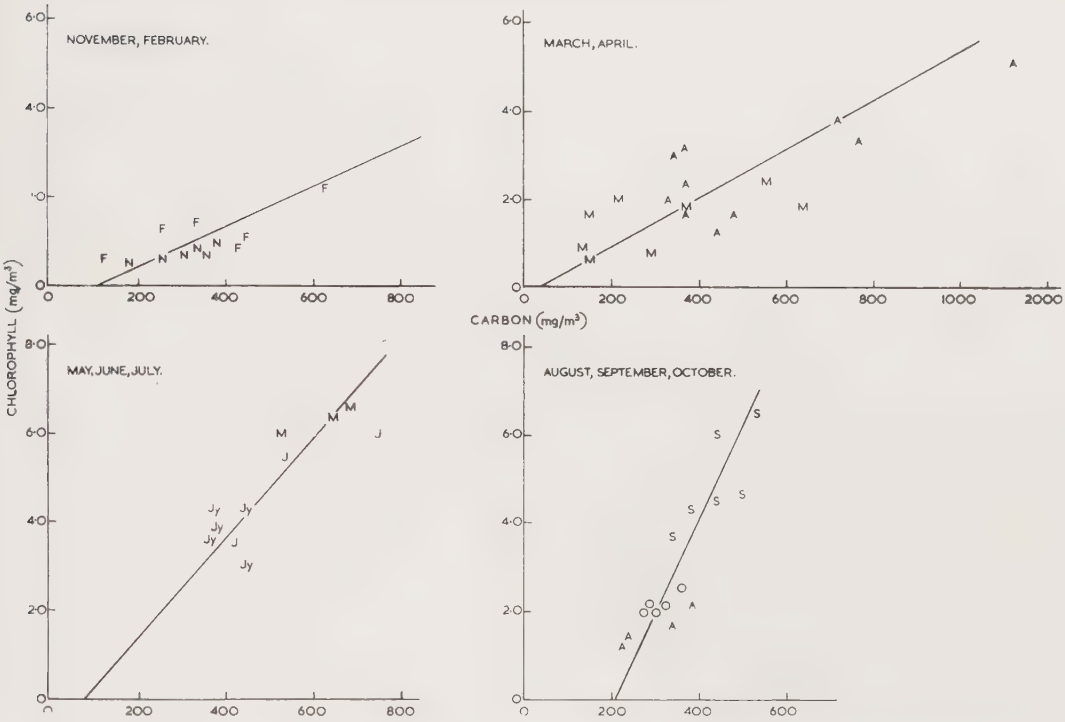


FIG. 3. Chlorophyll to carbon relations for Aberdeen Bay obtained by grouping all the values into seasons.

be a change in the slope between those for late summer and the remainder (a similar change will be seen in the data from Fladen). The simplest interpretation of these data is that all the chlorophyll is photosynthetically active. The alternative hypothesis, that there is always a fixed proportion of inactive chlorophyll, seems rather unrealistic.

The relations between chlorophyll and carbon are more difficult to interpret. Since the values obtained within any month tend to be fairly similar, any intepretation depends on the method of grouping data. The data have been divided into four groups roughly according to seasons (Fig. 3), and all the regressions are highly significant. These results can be interpreted as showing that the detritus is effectively zero in March–April, builds up to about 200 mg/m³ in the autumn and then decreases during the winter. The chlorophyll:carbon ratio in the plants appears to be very low in winter (1:213) and increases to a maximum (1:47) in the autumn. This implies that living plants form the most important part of the organic carbon in the water and provides an intuitively reasonable succession of events, with the low chlorophyll:carbon ratios in the winter the result of low light intensities, the increasing proportion of chlorophyll showing an increasingly active population, and the larger quantities of detritus following this increased growth.

Fladen

Sampling for temperature, salinity, phosphate, nitrate, chlorophyll and particulate carbon was carried out on Fladen once a month approximately, from March 1959 to January 1960. Generally, C^{14} samples from 0 to 50 m at 10-m intervals were exposed for 4 hr at 1000 ft-c and at sea-surface temperature; duplicate samples were used for an *in situ* half-day exposure. Extinction coefficients were determined with an underwater photometer (kindly provided by R. Holmes of the Scripps Institute) using a No. 45 Ko-

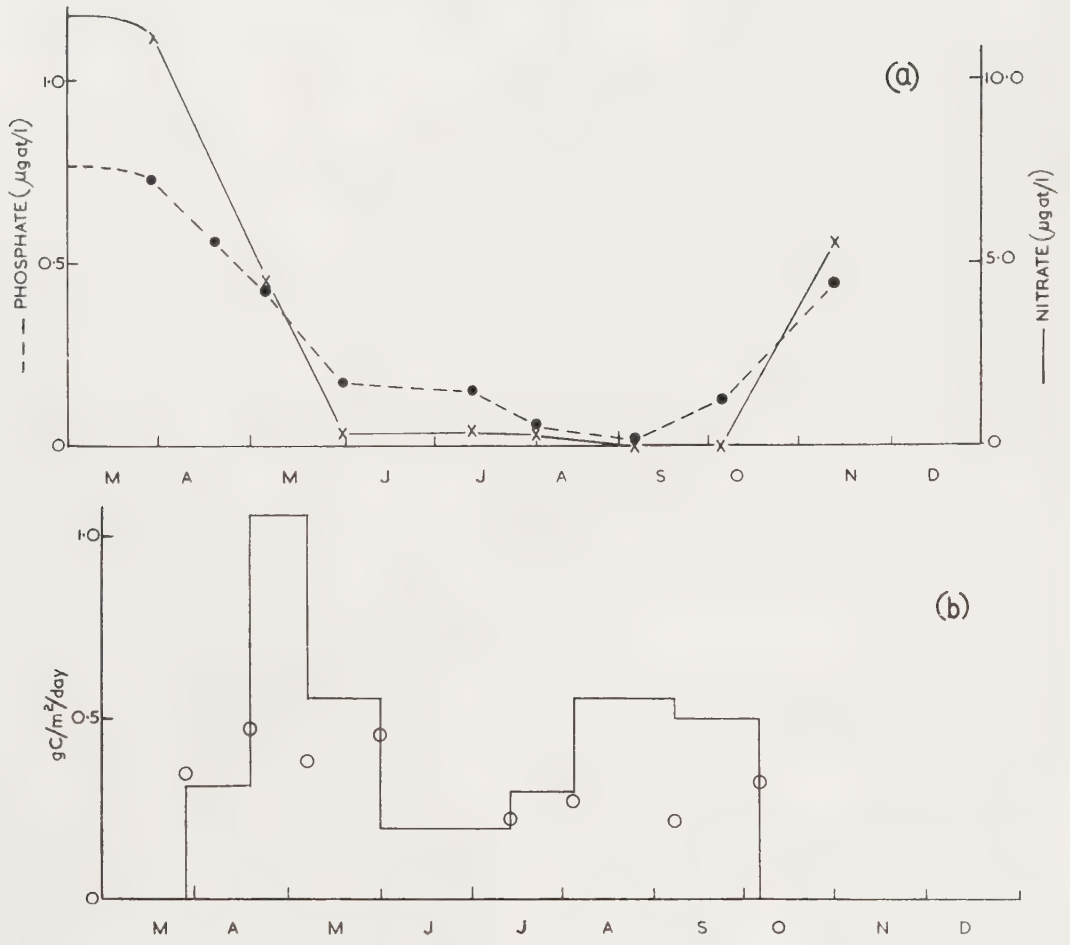


FIG. 4. Features of the seasonal cycle on the Fladen Ground. a) The changes in phosphate and nitrate at 10 m. b) The rate of production calculated from the phosphate data (histograms) and from the *in situ* C^{14} experiments (circles).

dak Wratten filter with maximum transmission at 480 mμ.

Figure 4 shows the cycle of nutrients and production. The production histogram was calculated from changes in phosphate (Steele 1956), and the production rates from the *in situ* C^{14} experiments are also shown.

The C^{14} to chlorophyll relations are shown in Figure 5. Again, the data have been divided into groups of months. The winter values (November, January and March) appear to have a lower slope than those for spring and autumn (April, early May, September and October). Generally there is no consistent difference in the slopes of samples from different depths but this is not true for certain values from late May, July and August. The depths at which these very low C^{14}:chlorophyll ratios were found are indicated in Figure 5 showing that they are all deeper samples. The values from 0–30 m for these months, however, have similar ratios, and a higher slope than for the other months. Thus the 0–30-m values show a similar trend to that found in Aberdeen Bay.

The results of the *in situ* experiments are given in Figure 6. The assimilation values per unit of chlorophyll are plotted on a logarithmic scale so that the lower parts of the profiles would be straight if the uptakes were proportional to light intensity. This obviously does not hold, especially during

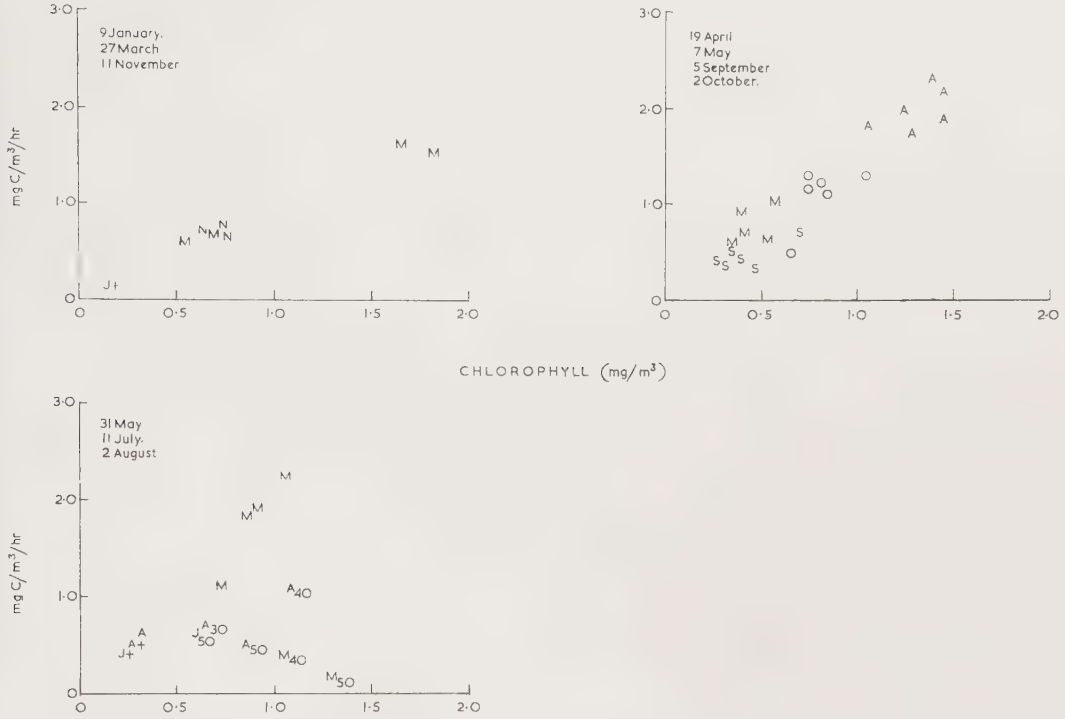


FIG. 5. Relations between carbon assimilation at 1000 ft-c and chlorophyll concentration on the Fladen Ground (+ indicates more than one value).

the summer, and Figure 6 also shows the assimilations plotted against relative light intensities, derived from the extinction coefficients at 20–30 m. Steeman Nielsen and Hansen (1959a) exposed duplicate samples from the same depth to a range of light intensities in an incubator and found that a linear extrapolation generally cut the carbon assimilation axis at a negative value which could be interpreted as an estimate of respiration. The results given here show that, with natural light conditions and with the different populations at different depths, the same type of results are obtained. There is also a slight suggestion that respiration may be higher during the summer when nutrients are scarce. On this basis the deeper chlorophyll samples during the summer would still represent living plants and so the low C^{14}: chlorophyll ratios obtained in the incubator would be caused by dark adaptation of plants whose vertical movement is restricted by the thermocline. This effect has been shown both by Steeman Nielsen and Hansen (1959b) and by Ryther and Menzel (1959).

The chlorophyll–carbon relations are given in Figure 7, and once more they have been grouped to show possible relationships. The January values were very low and so their "interpretation" is doubtful but they have been included with the spring data, Figure 7(a), which indicate a chlorophyll: carbon ratio of 1:76 with, apparently, little detritus.[1]

Since dark adaptation is often thought to be associated with an increased proportion of chlorophyll in the plants, the carbon samples corresponding to the low C^{14}:chlorophyll ratios in Figure 5 are indicated in Figure 7. In Figure 5 the most marked change was found in the samples on May 31, and in

[1] The carbon values for May 7 seem unduly low. On this occasion the titration blanks had a greater than usual variability between replicates. It is possible that all the values should be increased by 37 mg/m³ which would give better agreement. Also, the very high surface value has been ignored as probably due to contamination.

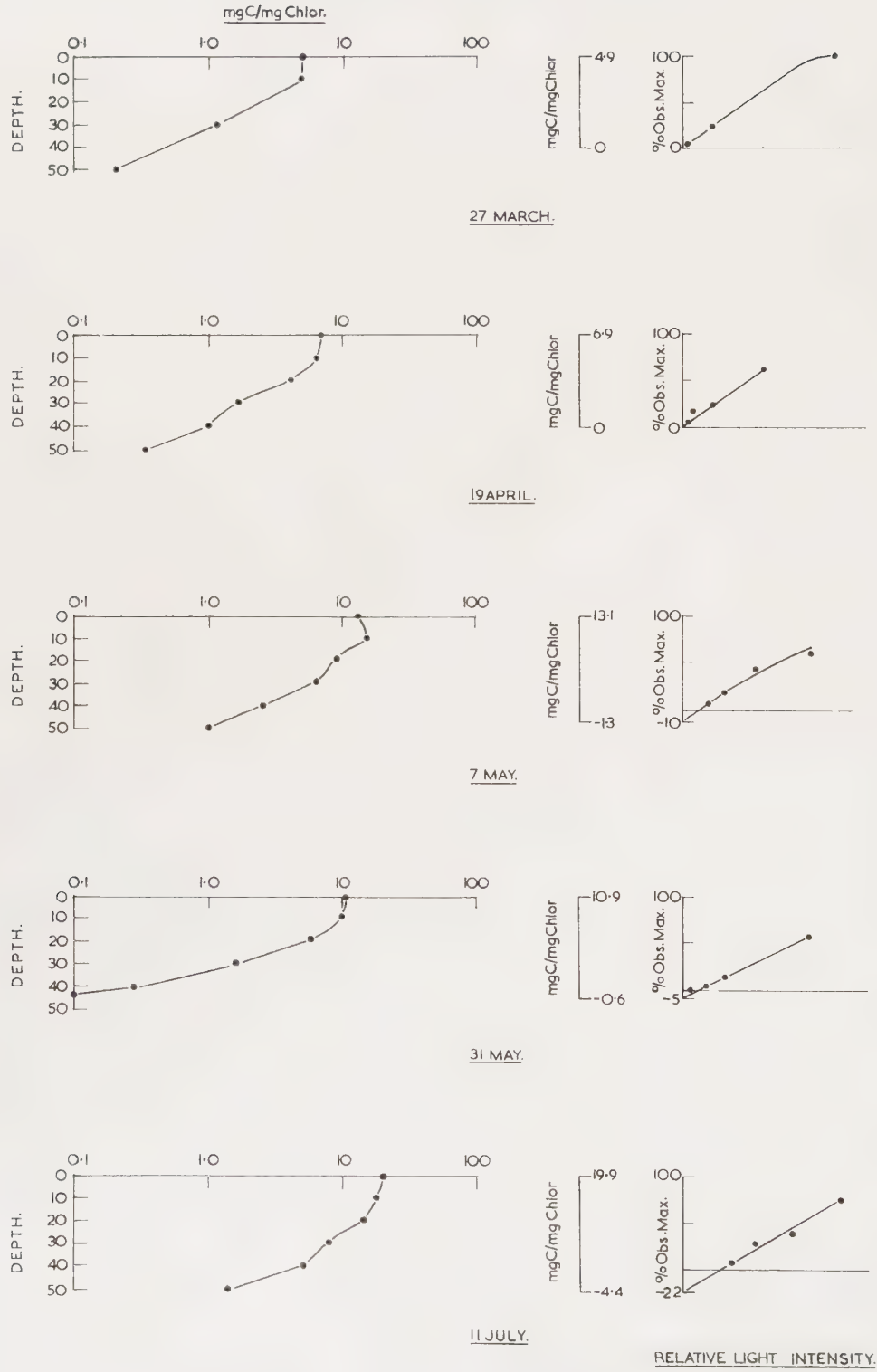
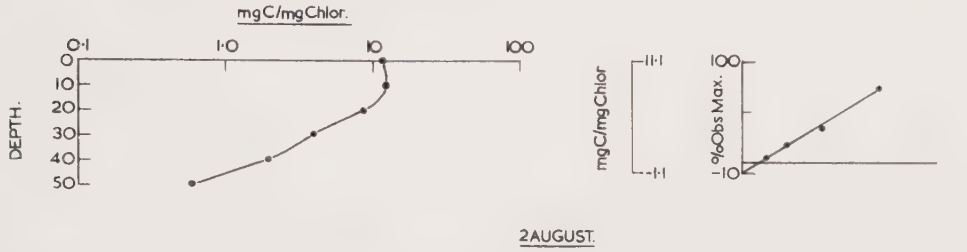


FIG. 6. Half-day *in situ* C^{14} experiments on the Fladen Ground. Left—assimilation per unit of chlorophyll, plotted against depth. Right—assimilation per unit of chlorophyll (also shown as percentage of the observed maximum) for the deeper samples, plotted against relative light intensity.



2 AUGUST.

5 SEPTEMBER.

2 OCTOBER.

11 NOVEMBER.

9 JANUARY.

RELATIVE LIGHT INTENSITY

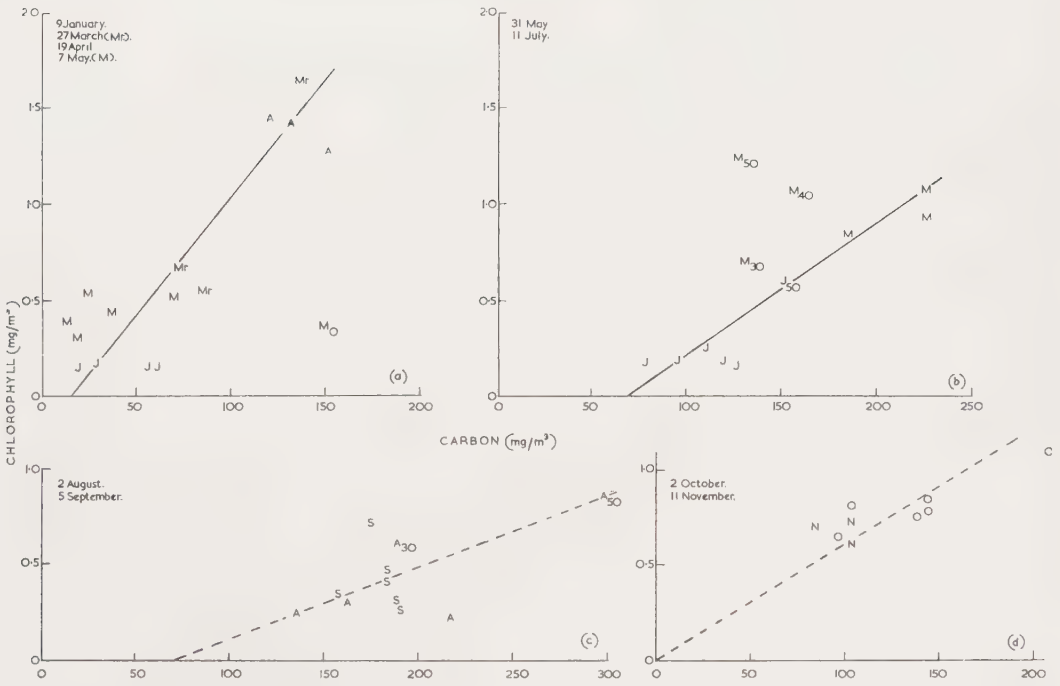


FIG. 7. Chlorophyll to carbon relations for the Fladen Ground obtained by grouping all the values into seasons.

Figure 7(b) these do show possible differences, but this is not found in the July or August values. For Figure 7(b) the line indicates the statistical regression excluding the deeper May samples.

For late summer a statistically significant regression is not possible. The dotted line in Figure 7(c) shows the relation that would hold if it is assumed that there is no significant increase in detritus during this period. This would imply that, during this period, the chlorophyll:carbon ratio in the plants has decreased considerably to about 1:260. In Figure 7(d) the dotted line shows the lowest possible chlorophyll:carbon ratio, 1:165, in the plants during late autumn, and this, in turn, implies that the ratio has increased again since late summer.

DISCUSSION

The C^{14} to chlorophyll relations are fairly satisfactory. The Aberdeen Bay data and those from 0–30 m on Fladen both show proportionality between C^{14} uptake and chlorophyll concentration. This suggests that effectively all the chlorophyll is contained in living plant cells. This does not agree with Gillbricht (1952) who calculated that for Kiel Bay only a small part of the chlorophyll was active. For the deeper phytoplankton on Fladen, immobility in the thermocline during summer may produce dark adaptation. If, as Ryther (1954) states, C^{14} uptake represents net production then the values computed from Figure 6 give respiration directly with a range from 0 to 22% of maximum production. Steeman Nielsen (1955) suggests however, that the negative values obtained here may represent only 60% of the respiration which would then vary between 0 and 37%.

The other interesting feature of the results is the variation in the C^{14}:chlorophyll ratio. Figure 8 shows the ratios from both areas corrected to 1000 ft-c. Both show the same variation by a factor of two but have their maxima at different times during the summer, so that light adaptation by itself would not seem a sufficient explanation. It is also important to note that the changes on Fladen

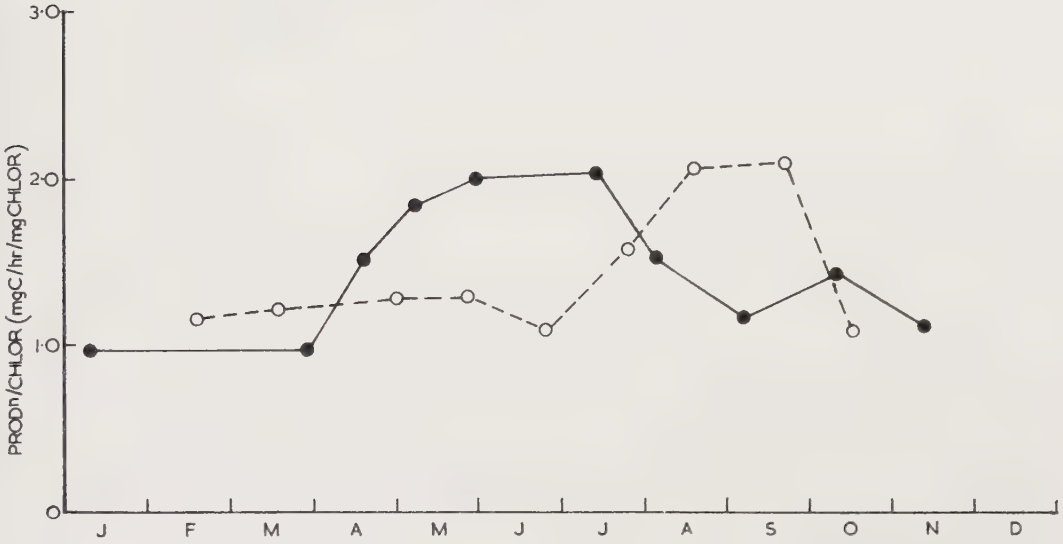


FIG. 8. The monthly average ratios of carbon assimilation per hour at 1000 ft-c to chlorophyll concentration; solid line, Fladen, 0–30 m; dashed line, Aberdeen Bay.

are roughly opposite to the changes in nutrient concentration (Fig. 4). Thus the variations in photosynthetic efficiency cannot be explained in terms of nutrient limitation.

The chlorophyll to carbon relations for Aberdeen Bay give intuitively reasonable results. The summer maximum in the plant ratio, 1:47, is close to that obtained by Riley. The analyses also imply that the plants form the largest part of the organic material, which is in disagreement with Gillbricht's results for shallow turbid water, but is in agreement with Parsons and Strickland (1959). For Fladen the results are less satisfactory and the implication of extremely low chlorophyll:plant–carbon ratios in the summer is very tentative although it might be linked with slow growth rates imposed by nutrient limitation.

Finally, Figure 9 shows the comparison of chlorophyll and carbon in Fladen and Aberdeen Bay. For Aberdeen Bay the general correspondence between these factors can be seen, but for Fladen the decrease in chlorophyll during the summer occurs when the carbon values are generally highest. Thus for any area, chlorophyll is not necessarily a good index of organic matter, nor are the ratios for different areas similar. The chlorophyll concentration in Aberdeen Bay during the summer is roughly ten times that on Fladen but the carbon is only about three times as great. This will be especially important in terms of the food concentrations that might be available for zooplankton.

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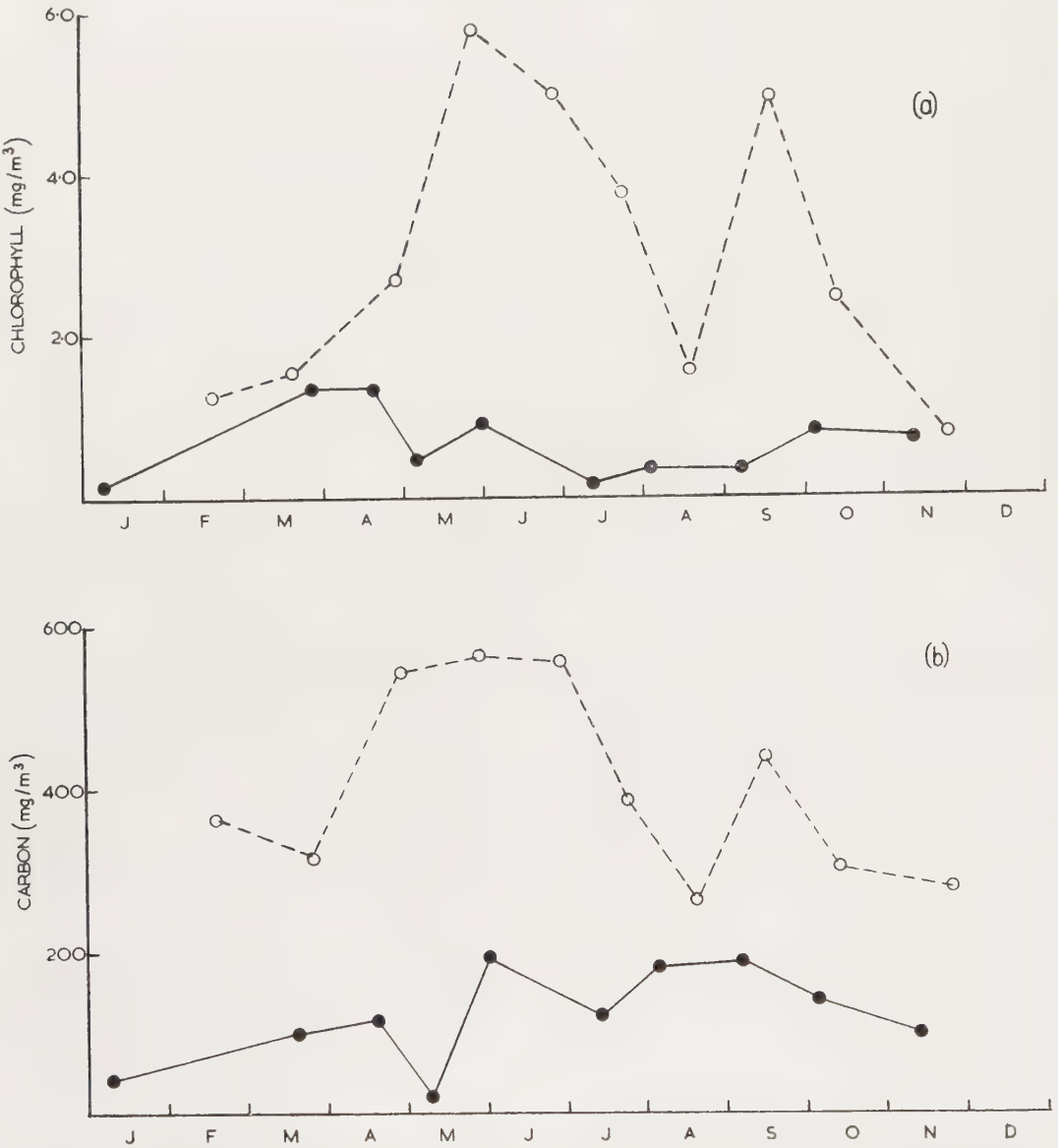

FIG. 9. The average concentrations of a) chlorophyll and b) particulate organic carbon for 0–30 m on Fladen (solid line) and in Aberdeen Bay (dashed line).

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NOTES AND COMMENT

Thurlow Christian Nelson

Marine Biologist

Dr. Thurlow Christian Nelson, marine biologist, was drowned on September 12, 1960, off a storm-swept shore near his summer cottage at Green Creek, Cape May, N. J., while trying to secure his rowboat against hurricane Donna. He would have been 70 years of age on September 22.

He was born in Highland Park, N. J., in 1890, and attended Rutgers Elementary and Preparatory Schools in New Brunswick, just across the Raritan River from his home. He was graduated from Rutgers University in 1913 with a B. S. in biology, and from the University of Wisconsin in 1917 with a doctorate in zoology and physiological chemistry. During World War I he served as a first lieutenant in the Army Sanitary Corps.

He was invited to the Rutgers teaching staff in 1919 as assistant professor of zoology; became associate professor in 1922; and professor in 1926. From 1925 to the time of his retirement in 1956 he was Chairman of the Department of Zoology, and was biologist in charge of shellfish investigation at the N. J. Agricultural Experiment Station from 1916 to 1950. In addition he served as Chairman of the N. J. State Water Policy and Supply Council from 1945 until his death. Following his retirement he was named Julius Nelson Professor of Zoology in the Rutgers Graduate School, a chair founded in memory of his father, Julius Nelson, who began oyster research in New Jersey for Rutgers in 1888.

In 1934 Dr. Nelson was honored as Rutgers' Distinguished Scholar and Gifted Teacher. Five years later the same university awarded him an honorary degree of Doctor of Science; and in 1958, the Rutgers Alumni Federation Award.

In *American Men of Science* Dr. Nelson's specialties are listed as biology of the oyster, estuarine ecology, marine biology, and limnology. His research in these areas resulted in more than 125 papers on the anatomy, physiology, and ecology of the oyster and associated organisms, parasitology, and water supply.

He held membership in many scientific societies. He served as president of the American Society of Limnology and Oceanography in 1953; was president of the National Shellfisheries Association 1931–33; treasurer 1939–41, and in 1948 vice-president of the American Society of Zoologists; was vice-president of the American Microscopical Society in 1941.

Viewed in perspective this long list of accomplishments is a singular one. But equally impressive were Dr. Nelson's contributions as a teacher over a span of some 45 years. His keen mind, warm personality, sincere forceful speech, genuine interest in people, and deep enthusiasm for biology, attracted many students to him. As an active church leader with deep sincere religious convictions, Dr. Nelson often wrote and spoke on the common ground of religion and science. He died in the midst of the elements which provided so much of the stimulus for his productive life. There was much of the old Viking in his Danish blood.

Melbourne R. Carriker

Department of Zoology, Chapel Hill, and Institute of Fisheries Research, Morehead City, University of North Carolina

Changes in pH and Total CO_2 in Natural Waters

Verduin (1960) apparently remains unconvinced that CO_2 changes cannot be interpreted directly from pH changes following addition of a strong base or strong acid, in spite of the categoric statement of Beyers and Odum (1960) that his contention is wrong theoretically and experimentally.

Some relatively simple chemical algebra can establish the difference between titration with a strong acid and titration with H_2CO_3. We need not put numerical values on alkalinity or pK's, except to state that $pK_2' - pK_1' = 3.0$. Start with a sample of sea water having a pH equal to pK_2'. By the definition of pK_2', the initial molality of bicarbonate ion, a, is equal to the molality of carbonate. Neglecting borate, the alkalinity is $3a$, the hydroxyl ion concentration being infinitesimal. Free carbonic acid is also infinitesimal ($10^{-3}a$), so total CO_2 is $2a$.

Now titrate with CO_2-free HCl until the pH is lowered exactly one unit. The ratio of bicarbonate to carbonate is now 10; the ratio of bicarbonate to carbonic acid is 100. Total CO_2, the sum of carbonic acid, A; bicarbonate, B; and carbonate, C, is unchanged; that is, $A + B + C = 0.01B + B + 0.10B = 2a$ from which $B = 1.80a$, $C = 0.18a$, and $A = 0.018a$. Alkalinity, $B + 2C$, has been reduced to $2.16a$.

Continue the titration until pH is lowered another unit. We now have $B/C = 100$, $B/A = 10$, and, assuming no loss of CO_2 to the air, $A + B + C = 2a$. We now find $B = 1.80a$ again,[1] $A = 0.18a$, and $C = 0.02a$. Alkalinity is now $1.84a$.

Now duplicate the titration with H_2CO_3 instead of HCl. When pH is lowered one unit, the ratios B/C and B/A are the same as at this stage of the other titration, but total CO_2 has increased. Alkalinity, however, has remained constant, since no strong acid has been introduced. We thus have $B + 2C = B + 0.2B = 3a$, from which bicarbonate is $2.5a$, carbonate is $0.25a$, carbonic acid is $0.025a$, and total CO_2 is $2.78a$.

When pH is lowered two units, $B + 2C = B + 0.02B = 3a$, or bicarbonate is $2.94a$, carbonate is $0.03a$, and carbonic acid is $0.29a$. Total CO_2 is thus $3.26a$.

Table 1 summarizes these results. It is clear that the mean slopes of the two titration curves, which, if expressed as equivalents per pH unit, are the same as the "buffer values" of Van Slyke (1922), are greatly different at different pH values, and that using moles per pH unit is no improvement.

These calculations all require that pK_1' and pK_2' remain constant during the titration. Remembering that $pK_1' = pK_1 + \log \frac{\gamma HCO_3^-}{\gamma H_2CO_3}$ and $pK_2' = pK_2 + \log \frac{\gamma CO_3^=}{\gamma HCO_3^-}$, we note that pK_1 and pK_2 are constant as long as temperature is constant—an easy condition to satisfy in the course of a titration—but that $\log \frac{\gamma HCO_3^-}{\gamma H_2CO_3}$ and $\log \frac{\gamma CO_3^=}{\gamma HCO_3^-}$, the ratios of activity coefficients, while relatively insensitive to temperature, are critically dependent on ionic strength (*i.e.*, salinity). In the case of sea water, if we titrate with an acid of twice the concentration of sea water (say, 1.4N HCl) the ionic strength is negligibly affected. One can do this with a large volume of sea water, say one liter, and a small burette, say 2 ml, being sure to stir adequately.

For fresh waters, however, it is not so easy to hold ionic strength constant. Consider, for example, the extreme case of a spring water containing only $NaHCO_3$ and Na_2CO_3 and that $a = 0.01$ molar, with initial conditions as in Table 1. The molarity of Na^+ is .03, and the initial ionic strength $\mu = 0.040$. Without changing the total volume add enough HCl to lower pH one unit; the conversion of $CO_3^=$ to HCO_3^- results in μ becom-

[1] Bicarbonate molality goes through a maximum at pH = ½ ($pK_1' + pK_2'$) and then decreases. At this pH, $A = C$; and under the conditions postulated ($pK_2' - pK_1' = 3.0$), $B/A = B/C =$ antilog $1.5 = 31.6$. Hence $0.0316B + B + 0.0316B = 2a$, or $B = 1.88a$, $A = 0.059a$, $C = 0.059a$.

TABLE 1. *Comparison of calculated buffer capacity in titrating sea water with HCl and H_2CO_3*

	Initial conditions pH = pK_1'	Conditions after lowering pH one unit		After lowering two units	
		Using HCl	Using H_2CO_3	Using HCl	Using H_2CO_3
Alkalinity	3*a*	2.16*a*	3.0*a*	1.84*a*	3.0*a*
Carbonate molality	*a*	0.18*a*	0.25*a*	0.02*a*	0.03*a*
Bicarbonate molality	*a*	1.80*a*	2.5*a*	1.80*a*	2.94*a*
Carbonic acid molality	0.001*a*	0.018*a*	0.025*a*	0.18*a*	0.29*a*
Total CO_2	2*a*	2.00*a*	2.78*a*	2.00*a*	3.26*a*
Moles CO_2 added		zero	0.78*a*	zero	1.26*a*
Equivalents H_2CO_3 added		zero	1.56*a*	zero	2.52*a*
Equivalents HCl added (equal to decrease in alkalinity)		0.84*a*	zero	1.16*a*	zero
Mean slope, equivalents per pH unit		0.84*a*	1.56*a*	0.32*a*	0.96*a*
Mean slope, moles per pH unit		0.84*a*	0.78*a*	0.32*a*	0.48*a*

ing 0.032. At a pH-lowering of two units, $\mu = 0.030$. In the case of sea water, log $\frac{\gamma CO_3^-}{\gamma HCO_3^-}$ has a value of about –0.57 at Cl = 1% ($\mu = .036$), and since log $\frac{\gamma CO_3^=}{\gamma HCO_3^-}$ is proportional to $\mu^{1/2}$, it can be computed that a change of 0.08 would result between $\mu = 0.040$ and $\mu = 0.030$, equivalent to a pH change of the same amount.

It can be argued that the empirical titration curve derived by the method of Beyers and Odum (1959) using CO_2 results in a curve of total CO_2 vs pH that is independent of pK_2' or log $\frac{\gamma CO_3^=}{\gamma HCO_3^-}$. However, such a curve can be used to study respiration or photosynthesis only if it is obtained in the same way that the organism under study adds CO_2 to the water. Specifically, to lower pH one unit in the case of the spring water just postulated would require the addition of 0.0075 moles of CO_2 per kg (0.75*a*, Table 1). At 28°C, a solution saturated with CO_2 at one atmosphere partial pressure is about 0.03 molal, so that we would have to add about 250 ml/L, increasing the volume by a quarter. Respiring organisms presumably bring about the same addition of CO_2 with negligible volume change.

Rigorously, therefore, the only way to prepare a CO_2-pH curve for fresh waters is to perform a sufficient number of analyses of total CO_2 at a given temperature on samples of the water to which only gaseous CO_2 has been added (or from which it has been swept out). Any change in total solids will require preparation of a new curve. Temperature must be fairly carefully controlled, or else a family of curves covering the desired temperature range must be constructed.

In the case of sea water, such curves can be derived by computation, using the apparent dissociation constants of carbonic and boric acids. The latter should not be neglected, especially for pH values greater than 8.0, and its second dissociation constant is also significant (Lyman 1957). The procedure is as follows:

Assume that we have a sample of Pacific surface water of Cl = 19%, with pH of 8.5, temperature 20°C. Values of the dissociation constants are for boric acid $pK_1' = 8.75$, $pK_2' = 10.08$; for carbonic acid $pK_1' = 6.01$; $pK_2' = 9.17$ (Lyman and Abel 1958). The specific alkalinity of this water would be 0.121 (Koczy 1956), giving 2.30 meq/L or 2.33 meq/kg of water. The boric acid would be 0.43 millimolal (Lyman and Fleming 1940).

At pH = 8.5, the borate alkalinity is

$$0.43 \times \left[\frac{1}{1 + \text{antilog}\,(8.75 - 8.5)} + \frac{1}{1 + \text{antilog}\,(10.08 - 8.5)} \right]$$

or 0.17. The remaining alkalinity, 2.16, is $B + 2C$. The other equation relating B and C is pH = pK_2' + log C/B, from which 8.50 = 9.17 + log C/B, or log C/B = –0.67 and $C/B = 0.214$. Substituting $C = 0.214\,B$ in the other expression yields $B = 1.51$ milli-

molal and $C = 0.324$. To obtain total CO_2, we need the value for A, from

$$pH = pK_2' + \log B/A.$$

Since $pK_1' = 6.01$, $\log B/A = 2.49$ at pH of 8.5; hence A is $B/310$ or 0.005. Total CO_2 thus is 1.84 millimolal.

Curves of total CO_2 as a function of pH for the appropriate chlorinities and temperatures can be readily constructed by this procedure. For following respiration or photosynthesis in sea water they are preferable to empirical titration curves, since no uncertainty resulting from volume changes is introduced. However, in their use it must be recognized that the CO_2-tension will be in equilibrium with atmospheric air at only one pH value, and that at other values there will be a tendency either to lose or take up CO_2.

In the case of fresh waters, the situation is not so easy as for sea water. It is clear from the above discussion that the apparent dissociation constants do not remain "constant"; hence empirical titration curves must be resorted to as described above. However, if one is equipped to perform enough gas analyses to construct the necessary curves, he might as well determine total CO_2 directly on all his samples and abandon precise pH measurements and the intermediate step of an empirical titration curve.

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Lyman's analysis of the titration with NaOH or HCl is based on relationships expounded in several papers in the literature to which I have referred frequently (Verduin 1956; Moberg *et al.* 1934; Moore 1939; and Dye 1944). However, Lyman has not presented any data showing that differential titrations in natural water agree with his computations.

The original paper by Beyers and Odum (1959) stated that differential titration with strong acid or base contained a "factor of 2" error. I submitted my note (1960) to point out the major source of their discrepancy, namely, the failure to recognize that a molecule of H_2SO_4 releases two molecules of H_2CO_3 from a bicarbonate solution. Beyers and Odum (1960) then presented a graph showing that HCl and NaOH stepwise titration curves deviated from their H_2CO_3 solution curve, in opposite directions. These deviations (much less than a factor of 2) may be partly attributable to the change in total alkalinity which I mentioned in my (1960) note, and which Lyman has computed, but according to Lyman's computation the slope of the NaOH curve, in the vicinity of pH 8.5, should be widely divergent from the other curves, because Beyers and Odum (1960) had titrated their sample from an initial pH of 5.6. Their curves, however, show close agreement in this region. I have never recommended carrying out a single stepwise titration over such a large pH interval. One can easily adjust the pH to a desired value by bubbling one's breath through a sample to lower the pH value, or by placing aquatic plants in a sample and exposing them to sunlight to increase the pH

value. Then, if one wishes to examine the CO_2:pH relationship over a wide range, this should be done in small increments to avoid altering the total alkalinity by more than a few per cent in any individual sample. Under such conditions the CO_2:pH relationship can be established with an accuracy of 95% or better by differential titration with strong acids and bases.

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CHLOROPHYLL *a* CONTENT OF INTERTIDAL ZONES ON A ROCKY SEASHORE

Recent evidence suggests that chlorophyll per square meter in communities adapted to similar light regimes tends to be roughly proportional to gross productivity, and is often not related to the size or taxonomic composition of the standing crop of producers (Gessner 1944; H. T. Odum *et al.* 1959). A universal feature of northern rocky coasts is the conspicuous zonation of intertidal life. As described by Stephenson and Stephenson (1949) three zones, an uppermost "black" or periwinkle zone, a middle barnacle zone and a lower "seaweed" zone, are generally recognizable anywhere in the northern hemisphere. The zones differ greatly in appearance and in species composition yet are exposed to similar light and nutrients, especially where the tidal range is small. The purpose of this note is to present data on chlorophyll extraction from a vertical series of samples to determine if chlorophyll concentrations throughout the intertidal region are similar, as might be expected on ecological grounds, or greatly different, as might be indicated by the diverse nature of the standing crops in the different zones. The study constituted one of the student-staff research projects which were a part of the 1957 Marine Ecology Course at the Marine Biological Laboratory, Woods Hole, Massachusetts. The authors are indebted to Charles S. Yentsch and John H. Ryther for suggestions regarding the quantitative estimation of pigments.

A stainless steel cylinder enclosing 25 cm^2 was placed over the surface to be sampled and all of the enclosed community removed with a putty knife; thorough scraping of the surface insured that all the algae were included. A total of 175 samples were taken at Nobska Point, a stony area east of Woods Hole, and from the "Spindal," a group of rocks in the center of Woods Hole harbor. Each sample was ground up in a mortar and pestle with organic-free sand, then extracted with successive washings of acetone. The acetone solution was then filtered, centrifuged and the chlorophyll *a* concentration determined photometrically after the method of Richards and Thompson (1952).

For purposes of comparisons we found it convenient to recognize four zones as follows. 1) The "black" zone, just above the mean high water level, in which the blue-green alga, *Calothrix crustacea*, was the chief producer. Coverage of rock surfaces by the encrusted bluegreens in this zone averaged 63% at Nobska according to un-

TABLE 1. *Average chlorophyll a in four zones in the intertidal region.*

Zones	No. of samples	Mean (g/m^2)	Standard deviation
1. "Black" (100% coverage)*	25	0.80 ± .009	0.48
"Black" (63% coverage)*	25	0.50	
2. Barnacle (100% coverage)	52	0.27 ± .001	0.19
3. *Fucus-Balanus* (100% coverage)	50	1.47 ± .051	0.86
4. "Seaweed" (100 % coverage)	50	1.04 ± .009	0.68
Mean of all zones	175	0.82	.52

* Two values are given for "'black" zone—one is the concentration within the patches of algae and the other value is average concentration for the zone as a whole (which is not completely covered by plants).

published data of Dr. E. T. Moul. 2) The "barnacle" zone with dense populations of *Chthamalus fragilis* and *Balanus balanoides* together with a few mussels (*Mytilus edulus*). A green alga, *Gomontia polyrhiza*, embedded in the tests of the barnacles and a bluegreen alga, *Rivularia* sp., attached to the barnacles or the rock surface were the chief producers of this zone. Coverage by barnacles and algae was generally 100% in this zone. 3) The *Fucus-Balanus* zone covered by *Balanus* (including associated algae) and masses of the brown alga, *Fucus vesiculosus*; coverage was generally 100%. 4) The "seaweed" zone below mean low tide and covered by masses of large algae such as *Chrondris crispus*, *Ceramium rubrum*, *Polysiphonia denudata* and *Dasya pedicellata*, with *Chrondris* usually forming the bulk of the standing crop; coverage was generally 100%.

Table 1 shows the average chlorophyll content in grams per square meter of the biomass in each of the four zones. These data indicate a fivefold difference with the lower zones having the largest amount. However, even the barnacle zone had appreciable amounts of chlorophyll as a result of the small algae associated with the more conspicuous animals; it is by no means just an "animal" zone as the name might indicate. It is also noteworthy that the very small

TABLE 2. *Inter-zone comparison of chlorophyll content in grams per square meter*

Zones compared*	difference	S.E. of differences	t	P
1 vs. 2	.23	.03	7.4	>.01
1 vs. 3	.87	.12	7.2	>.01
1 vs. 4	.54	.14	3.9	>.01
2 vs. 3	1.19	.13	9.6	>.01
2 vs. 4	.76	.03	24.6	>.01
3 vs. 4	.43	.16	2.8	>.01

* See Table 1 for names of zones.

standing crop of *Calothrix* had almost as much chlorophyll as the very large masses of seaweeds in the lower zones.

When the amount of chlorophyll in communities on rock surfaces of five different exposures,—namely, north vertical, south vertical, east vertical, west vertical and horizontal,—in each zone were compared, the maximum intrazone differences were not statistically significant at the 99% level. Differences in light and other factors apparently were not great enough to produce a measurable difference within the zones. However, as shown in Table 2 differences between zones were significant, the two lower zones being the most similar to each other. The mean chlorophyll concentration of the entire intertidal region was 0.82 g/m^2.

Published values for chlorophyll per square meter range from less than .01 g/m^2 in infertile open oceans to 3–4 g/m^2 in fertile aquatic grass, marsh or terrestrial communities. Odum *et al.* (1958) have classified communities into four types with respect to light intensity-chlorophyll adjustments: "(1) stratified communities with levels of light-shade adaptation. (2) shaded communities. (3) mixing communities with plant cells exposed to fluctuating light intensity. (4) bright, thin communities without shade adapted parts." Since shade adapted plants develop relatively more chlorophyll the assimilation number (ratio O_2 produced/chlorophyll) tends to be lowest in shaded communities, highest in thin communities and intermediate in stratified communities. The upper two intertidal zones appear to be the "bright thin" types while the lower zones approach the stratified type

since the seaweed mass has appreciable thickness and is partly shaded by water. Total area chlorophyll ranges from 0.01 to 0.60 g/m^2 in thin communities, and from 0.4 to 3.0 g/m^2 in stratified communities, according to data summarized by Odum *et al.* Since our values for the rocky intertidal (Table 1) are towards the upper range for these two types of community, moderate to high productivity is indicated. Furthermore, it is evident that the greater concentration of chlorophyll in the lower zones does not necessarily indicate greater potential primary production since we would expect more chlorophyll in the lower zones even if average oxygen production was the same as in the upper zones. In other words, chlorophyll differences, while statistically significant, may not be ecologically significant.

Assuming that the assimilation number is likely to be higher in the upper zones, then the data on chlorophyll content indicate that the entire intertidal region has approximately the same potential primary production irrespective of kinds or sizes of standing crops. Actual measurements of oxygen production will need to be made before this tentative hypothesis can be tested.

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Modified Van Dorn Water Sampler

Van Dorn (1957) described a plastic water sampler which is relatively inert chemically, free flushing, and can be messenger activated. He used rubber "force cups" for closures, commonly known as "plumber's friends." We have devised a sampler of similar design but with improved rubber ball closures that eliminate malfunctions due to improper seating of the force cup closures. This sampler consists of Plexiglas tubes, 20 in. long with an outside diameter of 4.5 in. and a capacity of approximately 4 L (Fig. 1).

For van Dorn's closures we substituted 4.5-in. rubber balls, molded from gum rubber with ¼-in. holes through the center. Neoprene or other similar lighter weight derivatives would be preferable if available. The most desirable feature of these ball closures is that they remain completely spherical after repeated use and form a perfect seal with the rims of the plastic sampling container. For a better fit and less wear on the surgical rubber tubing connecting them, the inside rim of this sampler was machined to a 30° bevel and the outer rim sanded. The balls were connected to the rubber tubing as follows: one end of each ball hole was countersunk for ½ in. to a diameter of 9/16 in. The head of a 5-in. ¼-20 brass bolt was inserted ½ in. into the end of a 10-in. piece of 5/16 × 3/32-in. surgical rubber tubing and held by a ligature of nylon thread. The bolt was passed through the ball hole and secured by a nut after a 1-in. micarta washer was first placed over the threaded bolt. By tightening the nut, the end of the rubber tubing was forced back against the walls of the countersunk 9/16-in. hole to form a tight non-metallic seal. Loops of Steelon wire were fastened to the upper part of the closures and inserted in the "U" head of the tripping rod in the cocked (pretripped) position (Fig. 2). The ball closures were then outside the sampling container and permitted complete flushing. For more durability

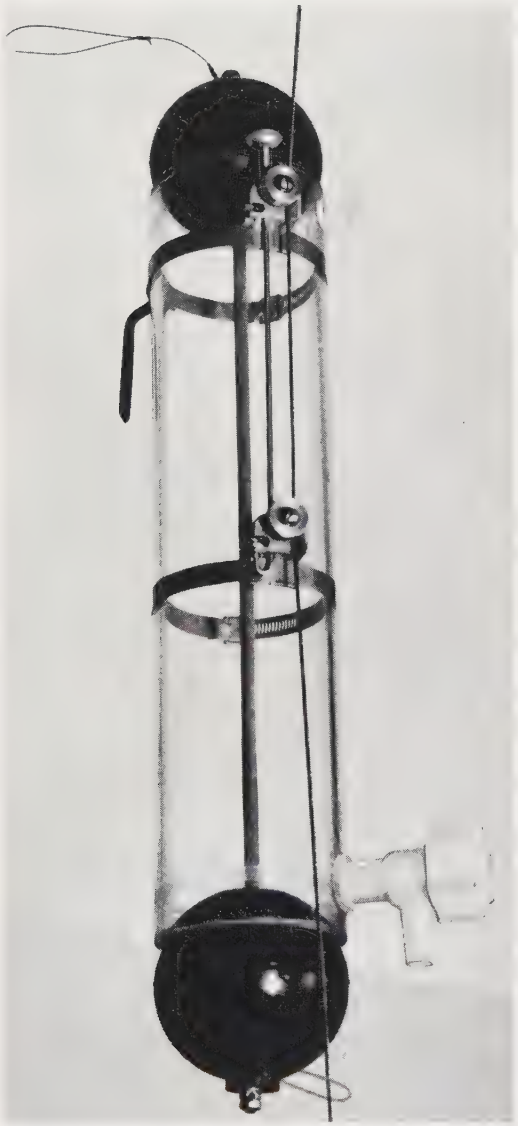

FIG. 1. Four-liter water sampler in closed position showing the attachment and tripping assemblies. Ball closures are held in place by tension of surgical rubber tubing.

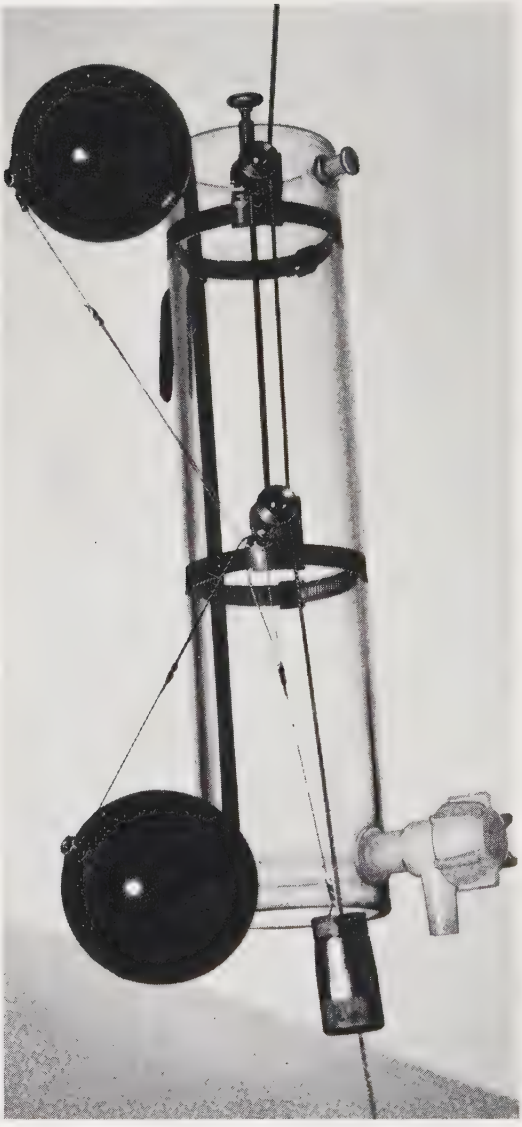

FIG. 2. Four-liter water sampler in a pretripped position showing wire loops from closures inserted in "U" bend of tripping rod and messenger attachment.

the sampling container can be made from polyvinyl chloride instead of the acrylic resin (Plexiglas) tubing used by van Dorn. Although polyvinyl chloride is extremely resistant to cracking and breakage, it is opaque, making it impossible to view the water level through the walls of the sampling container. Both plastics can be sawed and machined easily. We used Nalgene[1] ½-in. threaded spigots with a Teflon "O" ring for draining and ¼-in. Nalgene plugs for venting our samplers. These proved more efficient in operation than latex hose equipped with pinchcocks. When available,

[1] The Nalge Company Inc., Rochester 2, New York.

stainless steel bolts and nuts can be used instead of brass.

To attach these water samplers to the hydrographic wire, specially designed attachment and release assemblies were made for us by the Hytech Corporation.[2] These units consist of two cadmium plated irradiated brass castings provided with knurled stainless steel knobs, which tighten directly on the cable. This clamp can be used with any hydrographic cable between 3/32- and 7/32-in. diameter. A stainless steel ¼-in. tripping rod with cadmium plated button and "U" head comprises the release assembly. This rod is 9 in. long from center to center of the clamp castings. The lower clamp assembly was used for both the release of the messenger as well as the wires for the closing valves. These attachment units provide stability on longer bottles and aid in supporting the weight of larger samplers. Two aeroseal stainless steel hose clamps were used to fasten the attachment and release units to the samplers. For rack storage a handle was riveted to the upper aeroseal clamp.

These sample bottles are inexpensive to construct and permit multiple water samples to be made on one hydrographic cast. They are especially suitable for shallow water operation, where incomplete flushing of Nansen or similar water samplers may occur. Furthermore, the large capacity of the unit provides ample water for chemical and biological analysis.

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SIMPLE MECHANICAL AID TO LIMNOLOGICAL SAMPLING

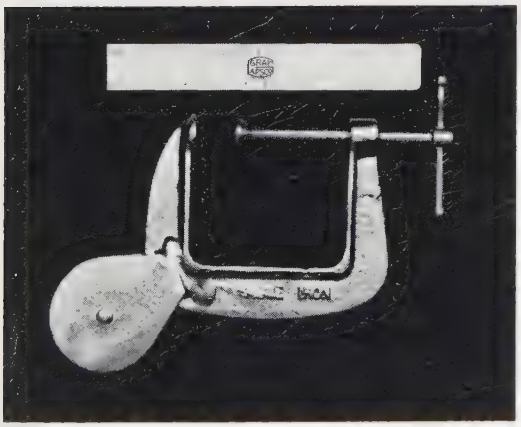

FIG. 1. Pulley and clamp.

Aquatic biologists are frequently confronted with the problem of lowering and raising heavy sampling equipment from small boats; there is a need for mechanical aid regardless of the size of the program. To meet this requirement a device was constructed which is inexpensive enough to justify its use in the smallest of sampling programs; and yet, is sufficiently strong to aid in more extensive field operations.

The machine is designed for temporary attachment to a rowboat or similar craft having rigid gunwales. The instrument consists of two lightweight, compact parts. The components, which may be obtained in most hardware stores, are a 2-in. awning pulley and a 2½-in. C-clamp. The part of the pulley frame which housed the eye was removed to form a slot. The pulley was then brazed to the clamp at an angle of 45° to the clamp screw. (Fig. 1.)

The unit is secured to the gunwale of the boat as shown in Figure 2. In operation, several pieces of limnological sampling equipment may be used with the aid of a single pulley. Moreover, since the pulley wheel is exposed on the upper side of the unit there is

FIG. 2. Apparatus in use.

no need to thread the lines through the implement before each operation. An arrangement such as this is essential when the lines or cables cannot be readily detached from their respective instruments, *e.g.*, electric thermometer cables, and wire or fabric lines upon which messengers must travel. Although no mechanical advantage is gained when using the unit, the direction of force is changed so that the weight of the sampling apparatus is supported by the side of the boat.

The pulley-clamp unit is inexpensive, thus it may be used to greatest advantage in projects that require repeated sampling on a limited budget.

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AN UNUSUAL LAKE OF THE ADIRONDACK MOUNTAINS, NEW YORK

Honnedaga Lake possesses many unique features: water clarity and color of high alpine lakes, acidity and low total alkalinity of bog lakes, temperature and oxygen relations of a miniature Finger Lake (New York). A once varied fish fauna has naturally disappeared leaving only a single indigenous species.

Originally known as Jock's or Transparent Lake, the name was later changed to the more euphonius "Honnedaga," allegedly the local Indian name for "clear waters." (According to Mr. E. A. Bates, Advisor in Indian Extension, Cornell University, a more literal interpretation is "calm waters.") The lake lies at an elevation of 2300 ft in the southeast corner of Herkimer County, in the southwest Adirondack Mountains of New York. In 1890, Honnedaga Lake was acquired by the Adirondack League Club, an organization that has maintained control of the property to the present time. The writer was first startled by the conditions encountered during a routine fishery survey in 1951

and none of the observations carried out since, nor discussions with more experienced limnologists, has lessened the original impression of uniqueness. Detailed limnological studies are not yet available but it is worth while to call attention at this time to responses of fish to the general conditions encountered.

The lake has an area of 770 acres and maximum depth of about 180 ft, with most of the narrow basin over 50 ft in depth. The watershed is comparatively small, about 3300 acres.

The most obvious of the physico-chemical characteristics is the transparency, which is about 75 ft (Secchi) and the apparent cobalt-blue color. Hydrogen-ion readings have varied from pH 4.8 to 5.8 and total alkalinity ranges around 2 ppm. Resistivity readings at 24°C are usually 40,000 to 44,000 ohms/cc.

Apparently brook trout (*Salvelinus fontinalis*) were the only native fish, an inference made on the basis of stocking and other records maintained from an early date by the Adirondack League Club. A falls on the outlet was probably a barrier to the passage of other species of fish in the watershed (Mohawk River drainage, via the West Canada Creek). In any event, lake trout (*Salvelinus namaycush*) were introduced by 1890 and three additional species were planted and established as forage species (white sucker, *Catostomus commersoni*; frostfish, *Coregonus cylindraceum quadrilaterale*; and cheek chub, *Semotilus atromaculatus*). Rainbow trout (*Salmo gairdneri*), salmon (*Salmo salar*), and smelt (*Osmerus mordax*) were also planted, but there is not such definite evidence that these species were established. An annual "sucker run" to one of the tributaries near the main club house, dead frostfish trapped against an outlet screen, and the practice of trapping chubs for bait are events that fix the establishment of the other species beyond doubt, however. Lake trout are recorded in the Annual Reports of the Adirondack League Club starting in 1896 and continuing through 1935. These fish often attained 10 lb in weight with an average weight of 3.1 lb for several hundred trout taken during this period. This may be compared with averages of 1.6 lb and 0.9 lb for two other Adirondack lake trout waters on the club during the same period.

The startling, and unique feature for such a large body of water, was the complete lack of all species save brook trout in several test nettings made since 1951. Interviews with guides and members make it clear that suckers, frostfish and chubs disappeared rather suddenly in the late 1920's or early 1930's. No source of information suggests that a visible fish kill occurred, however. Lake trout persisted for some time thereafter but specimens in later years were large headed and emaciated. No lake trout showed in the test netting but dead specimens were collected shortly after "ice out" in 1954 by former Honnedaga Lodge Manager, Mr. Jay Shaeffer of Old Forge, New York. All were yearling trout about 5 in. long and recently dead. It is clear that if lake trout are not now extinct, they are of low abundance.

The sequence of events describing the successful establishment of at least four species for a period of 30 to 40 years and their abrupt disappearance, suggests the development of incompatible environmental conditions. This is borne out by current tests to achieve satisfactory survival in stocked fish. Several series of trials with caged hatchery fingerling and yearling trout have shown identical results with complete or nearly complete mortality of hatchery fish in 12 to 24 hr, whereas native fish, seined from the lake or tributaries and used as controls, have survived. Lethal conditions appear limited to lake water as most hatchery fish survive in some tributary streams. Within the independent observations available, two exceptions exist. One suggests the development of temporary conditions permitting successful survival. The other indicates that trout acclimatized in certain hatchery water sources can make a satisfactory transition to Honnedaga Lake water.

In the first instance, tests were made with brook trout fingerlings from a nearby soft-water hatchery. Caged trout introduced in

July through September, 1957, gave negative survivals. However, a test in late November showed nearly complete survival over a one-week period. On the basis of this, a planting with marked fish was made, and survivors were collected in 1958 and 1959.

The second instance, trout from two hardwater and one softwater hatchery were used as test fish (generally 25 specimens per test). Fingerlings from eggs of native Honnedaga Lake parents, as well as a domestic strain of trout, were available from the hardwater hatcheries. Trout from one hardwater hatchery (Ithaca) all survived, whereas trout from the others perished (3 of 16 fish alive from softwater hatchery). In a later test, "conditioning" of trout at the Ithaca hatchery for several days resulted in satisfactory survival of trout from both of the other hatcheries.

Survival of brook trout fry in various stages of yolk sac absorption gave similar although somewhat delayed results. Wild fry were dug from redds in early April; five healthy fry were placed in containers containing the following Adirondack lake waters: 1) East Lake, the parent water as a control; 2) Little Moose Lake, a large neighboring lake, with abundant fish population, resistivity of about 13,000 ohms; 3) Honnedaga Lake; 4) Honnedaga Lake tributary. After five days, 4 of the 5 fry were dead in the last two groups, none in the first two; at 10 days, when the test was terminated, one of the control fish was dead. The mortality records were maintained by Miss Norma Smith, Little Moose Lodge, Old Forge, New York.

Many Adirondack lakes will not support fish life apparently because of inherent lethal water quality or because of inability of introduced fish to make the physiological adjustment to a different water quality. Presumably great differences in the buffering capacity of the water involved would seem a logical explanation in some instances, but the presence of toxic conditions cannot be ignored. A preliminary spectrographic analysis of Honnedaga Lake water, for example, indicated an unusually high zinc content (analysis courtesy, Dr. A. W. Laubengayer, Department of Chemistry, Cornell University). The toxicity of low concentrations of zinc in acid waters is well known (Brown *et al.* 1957). It is certain that the native Honnedaga trout are tolerant to conditions that cannot be endured by most introduced groups and that the intolerable conditions were acquired (at least currently) within the past few decades. Evidence now available is insufficient to explain the observations on survival of test fish. More detailed measurements of seasonal variation in water chemistry and survival of various groups of test fish are currently in progress.

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A Simple Method of Measuring Beach Profiles

For at least 15 years the writer has measured profiles of beaches using a simple rapid method. Other students of beaches have frequently inquired about the method and its accuracy, indicating that the method is not well known. This summary is intended to satisfy both kinds of requests.

The method requires only two wooden rods, each 5 ft long and about one inch by one inch in cross-section. Notches are cut at 1-ft intervals along each rod, with smaller notches at $\frac{1}{10}$-ft intervals throughout at least a foot at one end. A minor elaboration is a small wooden pad about 4 in. square nailed to one end of each rod to prevent the rod from sinking into loose sand.

In use, the rods are held vertically one rod length apart in a line to be extended across

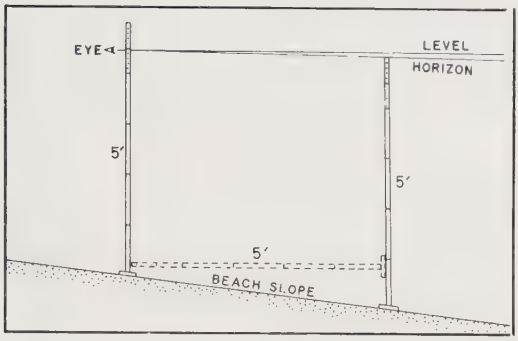

FIG. 1. Sketch of equipment—two wooden rods 5 ft long and marked off in feet and tenths of feet—used for measuring profiles of beaches.

the beach. The observer holding the landward rod aligns his eye with the top of the seaward rod and the horizon. He then reads and records the distance down from the top of his own rod of the point which is intersected by this line of sight (Fig. 1), interpolating to hundredths of a foot. Assuming the line of sight to be level, this distance is a measure of the difference in elevation of the beach at the two points that are 5 ft apart (in the example of Figure 1, the difference in apparent elevation is 0.53 ft). Where the beach has a backslope, the difference in elevation can be read by the same observer by aligning the top of his own rod with the horizon and reading the intersection on the seaward rod. To continue the profile, one of the rods is moved to a point 5 ft on the opposite side of the other rod and a second reading is made. Profiles can be measured either by moving the rods toward the sea or away from the sea. For fixing the direction of slope the convention has been adopted of noting the differences in elevation as minus or plus according to whether the leading rod is lower or higher than the following one. Finally, the differences in elevation are summed up and plotted against horizontal distance in order to obtain a profile across the whole width of the beach.

Usually the profiles extend from the base of a sea cliff or a point on the landward side of a beach to below water level. True elevation sometimes can be determined from a convenient bench mark, but more commonly it must be estimated from the depth of water at the seaward end of the profile as compared with a table of predicted tide. Where comparison of profiles at different times is desired, it is often sufficient merely to relate each set of measurements to a stake or other permanent reference point.

As a test of the reproducibility and accuracy of the method profiles were measured three times, with three different readers, over the same line across a beach near Santa Monica, California (Fig. 2). The results (Table 1) show a surprising consistency, with readings across individual 5-ft sections having a mean difference of 0.013 ft and a maximum of 0.05 ft. The greatest differences occurred on the soft upper part of the beach where the rods could sink slightly, on the steeper part where a small difference of rod position made a large difference in elevation, or in the swash zone where water movement undermined the rods. When summed up as complete profiles (Table 1), the mean difference at any point was 0.035 ft and the maximum was 0.18 ft. The difference generally becomes greater with distance from the starting point because of the accumulative tendency of the errors; however, the maximum difference is less than twice the width of the line representing the profile on Figure 2.

For somewhat more precise work an allowance should be made for the fact that the line of sight to the horizon is not quite horizontal, owing to curvature of the earth surface. The angle between the horizon and a level line increases according to the height of the observer above the water, but on beaches this height is such that the angle is only a few minutes (Table 2). When curvature correction is applied to the measured profile, it is obvious that the true slope is slightly greater than the measured apparent slope. For the profile of Table 1 and Figure 2 the true slope is steeper by 0.12 ft in a distance of 160 ft, or by less than 0°03′. On profiles of several hundred feet length this correction may become important. Where the horizon cannot be seen, as from a lake beach, the true slope can still be obtained, but the approximate distance to the opposite shore or other reference point must

TABLE 1. *Comparison of beach profiles made with rods and and with plane table* (ft)

Horizontal distance	Rod readings A	B	C	Elevations from rods A	B	C	Variation A, B, C	Corr. for elevation per 5 ft	Cumulative Corr.	Corrected elevation C	Elevation by plane table	Elev. by rods minus Elev. by P. T.
0				15.00	15.00	15.00	0.00	0.005	0.00	15.00	15.00	0.00
5	−.36	−.35	−.35	14.64	14.65	14.65	.01	.005	.01	14.64	14.64	.00
10	−.22	−.23	−.24	14.42	14.42	14.41	.01	.005	.01	14.40	14.40	.00
15	−.12	−.13	−.13	14.30	14.29	14.28	.02	.005	.02	14.26	14.25	.01
20	−.05	−.06	−.06	14.25	14.23	14.22	.03	.005	.02	14.20	14.18	.02
25	+.01	+.01	+.01	14.26	14.24	14.23	.03	.005	.03	14.20	14.18	.02
30	−.13	−.13	−.13	14.13	14.11	14.10	.03	.005	.03	14.07	14.02	.05
35	−.08	−.05	−.06	14.05	14.06	14.04	.02	.005	.04	14.00	13.95	.05
40	−.20	−.20	−.21	13.85	13.86	13.83	.03	.005	.04	13.79	13.72	.07
45	−.21	−.20	−.20	13.64	13.66	13.63	.03	.005	.05	13.58	13.49	.09
50	−.49	−.50	−.50	13.15	13.16	13.13	.03	.005	.05	13.08	12.99	.09
55	−.69	−.68	−.68	12.46	12.48	12.45	.03	.005	.06	12.39	12.30	.09
60	−.76	−.78	−.77	11.70	11.70	11.63	.02	.005	.06	11.62	11.51	.11
65	−.70	−.70	−.70	11.00	11.00	10.98	.02	.005	.07	10.91	10.80	.11
70	−.76	−.75	−.75	10.24	10.25	10.23	.02	.004	.07	10.16	9.99	.17
75	−.64	−.64	−.66	9.60	9.61	9.57	.04	.004	.08	9.49	9.39	.10
80	−.95	−.93	−.94	8.65	8.68	8.63	.05	.004	.08	8.55	—	—
85	−.92	−.90	−.95	7.73	7.78	7.68	.10	.004	.08	7.60	—	—
90	−.72	−.74	−.74	7.01	7.04	6.94	.10	.004	.09	6.85	6.78	.07
95	−.68	−.67	−.69	6.33	6.37	6.25	.12	.003	.09	6.16	6.10	.06
100	−.63	−.64	−.66	5.70	5.73	5.59	.14	.003	.09	5.50	5.46	.04
105	−.57	−.56	−.57	5.13	5.17	5.02	.15	.003	.10	4.92	4.86	.06
110	−.57	−.57	−.58	4.56	4.60	4.44	.16	.003	.10	4.34	4.29	.05
115	−.52	−.52	−.52	4.04	4.08	3.92	.16	.003	.10	3.82	3.76	.06
120	−.46	−.45	−.46	3.58	3.63	3.46	.17	.002	.11	3.35	3.30	.05
125	−.42	−.41	−.41	3.16	3.22	3.05	.17	.002	.11	2.94	2.88	.06
130	−.38	−.38	−.38	2.78	2.84	2.67	.17	.002	.11	2.56	2.50	.06
135	−.33	−.33	−.33	2.45	2.51	2.34	.17	.002	.11	2.23	2.14	.09
140	−.30	−.30	−.31	2.15	2.21	2.03	.18	.001	.11	1.92	1.87	.05
145	−.29	−.30	−.29	1.86	1.91	1.74	.17	.001	.11	1.63	1.50	.13
150	−.24	−.21	−.20	1.62	1.70	1.54	.16	.001	.12	1.42	1.36	.06
155	−.22	−.20	−.19	1.40	1.50	1.35	.15	.001	.12	1.23	1.20	.03
160	−.17	−.17	−.16	1.23	1.33	1.19	.14	.001	.12	1.07	0.95	.12
165	−.14	−.17	−.14	1.09	1.16	1.05	.11	.001	.12			

be known in order to make the computations.

A check on the profiles which were measured with rods was made by a telescopic alidade on a plane table and a stadia rod. The result (Table 1) shows differences that are the same order as those between the results obtained with rods by different observers. The use of a surveyor's alidade or level avoids the problem of accumulated error inherent in use of the rods, but it is more subject to error of reading off elevation. Usually where an alidade or a level is used, the beach profile is drawn on the basis of fewer points than are obtained with the 5-ft rods. In addition to their greater speed, the wooden rods are useful in remote areas where heavier and expensive surveyor's instruments may not be easily available.

TABLE 2. *Correction for curvature of earth surface* (From Bowditch, American Practical Navigator)

Eye height (ft)	Angle to horizon	Vertical difference for 5 ft horizontal distance
0	0°00′00″	0.0000
5	0°02′11″	.0030
10	0°03′06″	.0045
15	0°03′48″	.0055
20	0°04′23″	.0063
25	0°04′54″	.0072

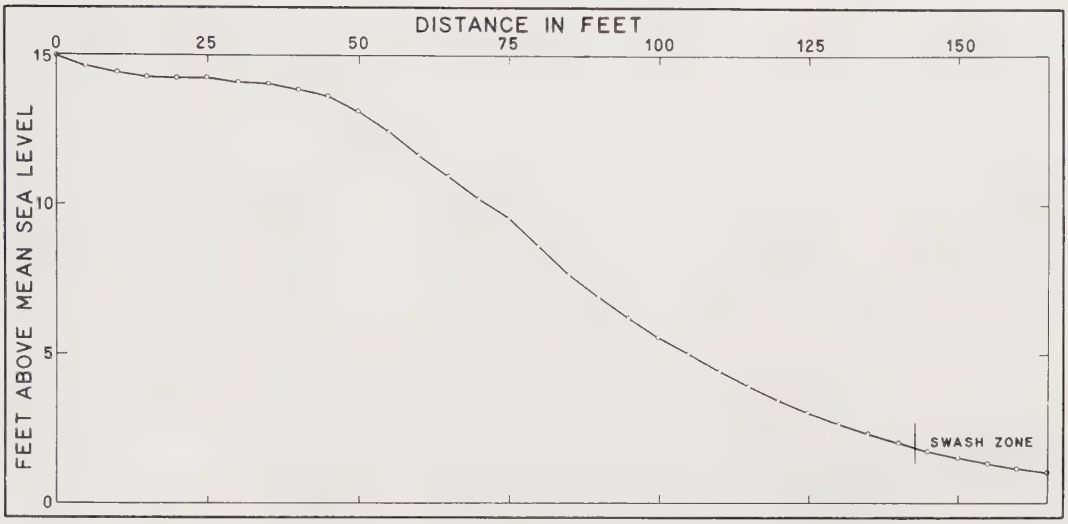

FIG. 2. Profile of beach at Will Rogers Beach State Park about two miles northwest of Santa Monica, California, the site of repeated measurements of Table 1. Based on measurements of Table 1 by observer C uncorrected for earth curvature.

It is possible that other workers may find the simple wooden rods useful for measuring profiles of beaches to determine seasonal and other cyclic changes with respect to waves, to relate slope to grain size of sand, and for other purposes. For most such objectives the method appears to possess sufficient accuracy, particularly in view of the fact that the presence of cusps and other irregularities produce local variations in profile which are greater than the error of measurement by the rods.

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THE STUDY OF IN-SITU MARINE PHOTOSYNTHESIS USING A LARGE PLASTIC BAG

Any precise study of the processes of phytoplankton growth and decay in the sea is impossible unless the same body of water is analysed over a protracted period of time. This necessitates some form of containment but the use of a tank has several disadvantages. Unless the tank is very deep the lighting of the water mass as a whole is unrepresentative of that found in the euphotic zone and the degree to which water in the tank is heated will generally be inadmissibly high. Finally no "balance" of dissolved oxygen or carbon dioxide can be readily computed using a shallow body of water with a large surface area in contact with the atmosphere.

We wish to report the construction of a piece of equipment the use of which has overcome the above disadvantages and which has enabled a study to be made of the growth and decay of marine phytoplankton under near "natural" conditions.

The equipment consisted of a thin plastic container connected to the atmosphere by a narrow neck, the body of the apparatus being some 6 ft beneath the surface of the sea so that much of the sun's heat was removed before reaching the container. To lessen the effects of wall growth and accidental contamination both the volume and the volume to surface area ratio of any container should be made as large as practicable. These facts and considerations of ease of construction, stirring and sampling suggested the use of a spherical bag at least 20 ft in diameter. In coastal waters it is doubtful whether increas-

ing the size of a bag by more than another 5–10 ft would have any advantage as for much of the time the bottom would then be beneath the euphotic zone.

The apparatus is shown in plan and to scale by Figure 1. A custom-made bag made of 8-gauge opalescent polyvinyl chloride sheet was used. The bag was exactly 20 ft in diameter, with an 18-in. diameter neck some 10 ft long and was supported by 6½-in. mesh netting of number 12 nylon seine twine. About 80–85% of the incident light was transmitted by this assembly. The netting was fastened to steel rings 10 or 20 ft in diameter, as shown, and the whole attached, by a steel "cradle," to a fiberglas buoyancy bell. The latter could be flooded with water or filled with air to counteract any increase or decrease in weight of the system brought about by salinity changes in the water surrounding the apparatus. (These changes are very considerable in British Columbia Coastal waters in the spring and a possible weight increase of up to 4000 lb had to be tolerated by the system). Weights were tied to the bottom ring of the apparatus after it was filled to ensure that no upthrust could develop on the buoy. The level of the buoy, and hence the bag, beneath the surface of the sea, was kept constant by adding or removing air as necessary (generally not more frequently than once a day).

The neck of the plastic bag was threaded up through the buoyancy bell and tied to the top. A fiberglas liner was then pushed down the inside of the neck and projected a few feet into the bag. This prevented the plastic from closing when density gradients in the water inside and outside the neck differed and it also lessened wear-and-tear on the plastic neck during sampling. At the end of an experiment the bag could be replaced without removing the whole apparatus. The bottom 10-ft diameter ring was removed, the old bag pulled through by SCUBA divers and a new bag, suitably folded, threaded through the neck of the buoy.

The whole equipment was anchored to three one-ton anchor blocks by three nylon ropes, about 150 ft long, fastened to halters on the central 20-ft diameter ring. The bag was thus at the center of an isosceles triangle, with the anchors at the three points, and was only able to move laterally within a circle of 10-ft or less radius.

The contents of the bag were kept stirred to uniformity to enable an accurate analytical balance of particulate and soluble material to be evaluated. The stirring was accomplished by an umbrella-like device, made of nylon and stainless steel, which opened on the up-stroke of a piston having a length of 2½–3 ft. An alternative arrangement with two "umbrellas," one at the top and one at the bottom of the bag, connected by rigid rod was also tried, the umbrellas being upside down so that they pushed water downwards. This latter system should, theoretically, give a greater upward velocity to water in the bottom part of the bag and hence better counteract the sinking of plant cells but there may be little to choose between the two arrangements.

The stirring motor, suspended on the buoyancy bell by a quadraped, was water driven from a pipe from the shore. It consisted of a reciprocating water motor similar to those used in water-powered washing machines. It was mounted over the neck of the bag in a vertical position with its piston rod projecting from the lower end.

In order to take samples the piston was stopped at the top of its stroke, the stirring line lowered into the bag and a meter block fastened to the quadraped. Water samples could then be taken from the center of the bag using standard Nansen or Van Dorn bottles. Light measurements were taken by lowering a light meter into the water and comparing the output with a "deck cell" placed on the buoy. "Light" and "dark" bottles for photosynthesis measurements could be fitted to the racks on the stirring assembly, as illustrated. With extinction values (base e) between about 0.3 and 1.0 it can be shown that the rate of photosynthesis in a bottle suspended 2 ft above the center point of the bag should approximate to the mean rate from a plant cell in random motion throughout the entire water mass.

Fouling of the outside of the equipment, with a consequent loss of light penetrating

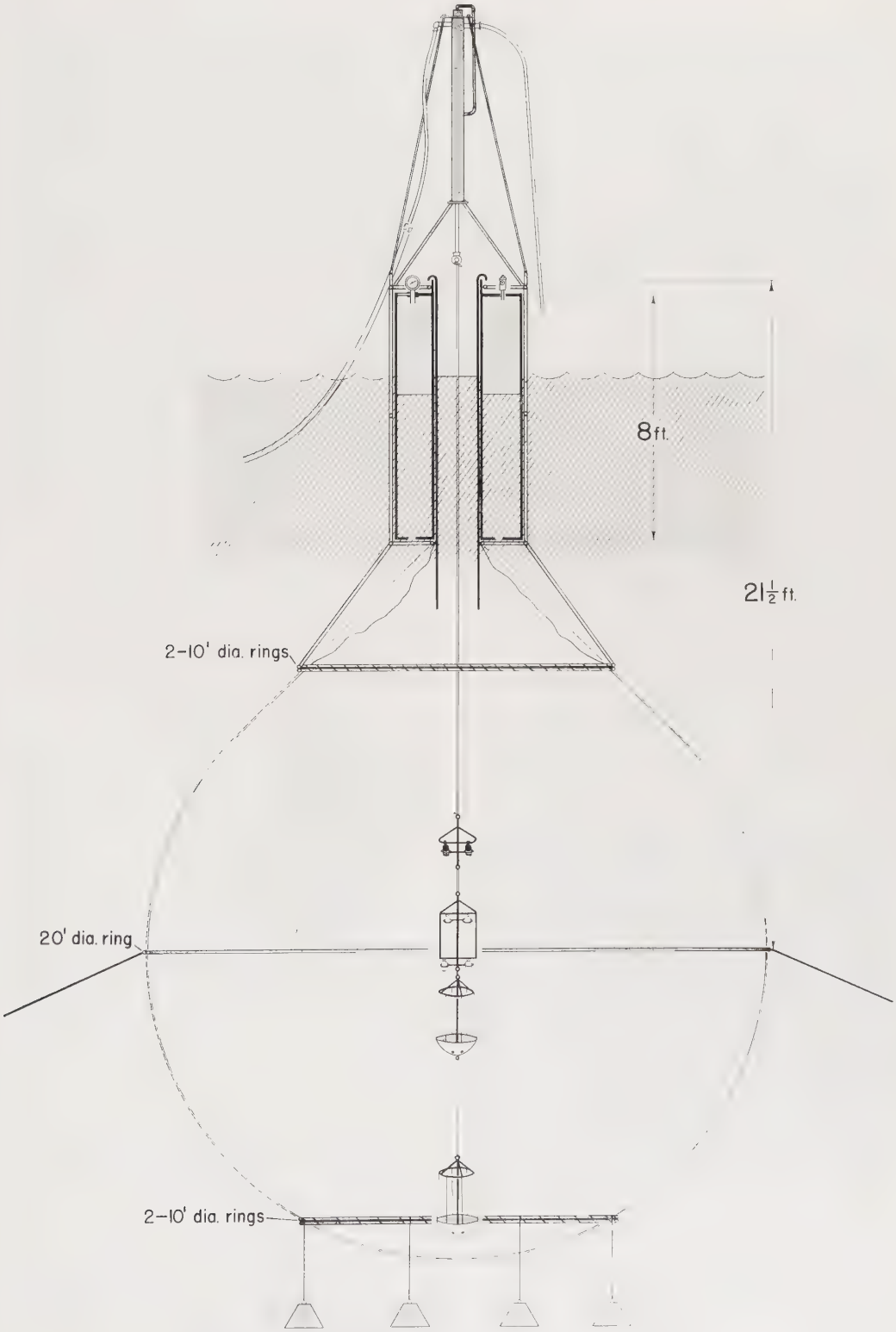

FIG. 1. Cross-section scale plan of plastic bag container.

into the bag, was restricted mainly to the upper surfaces and on the nylon netting. The growth, mainly a hydroid in our experiments, could be kept in check by throwing coarse crystals of copper sulphate onto the netting every few days.

We have used the above equipment successfully at Departure Bay (near Nanaimo, B. C.) where it was anchored some 300 ft from the end of a pier in water having a depth of at least 11 m at low tide. Full details of this work will be published later. In our experiments the bag was filled with water (32,000 U. S. gal) taken from a plastic pipe from a depth of over 20 m and filtered through a commercial diatomaceous earth filtration unit which removed all plant and animal life. The same water-line as that used to power the stirring motor was used for transporting water to the bag. The container was "innoculated" with a few hundred gallons of surface water, filtered through a 300-μ nylon net to remove most zooplankton. No animal populations were found to develop in the ensuing weeks. The temperature of the water in the bag kept to within 1°C of the temperature of the surrounding sea and the assembly appeared to be "seaworthy" to a remarkable extent, although it clearly should be used only in relatively sheltered waters.

We have reported the construction of this equipment so as to point out its proven feasibility. The apparatus is a most valuable tool for the study of primary productivity and could have many other applications, such as a study of zooplankton growth and grazing rates. We would be pleased to provide more detailed information to anyone contemplating the construction of a similar apparatus.

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Screened Pail for Sifting Bottom-fauna Samples[1]

Rawson (1953) described a screened pail which he used to process bottom samples. The following modified version of Rawson's pail has proved very satisfactory during 3 years of bottom fauna work on the Mississippi River. The metal paddles which were mounted on the inside of Rawson's pail have been replaced by a stationary propeller beneath the screen bottom of the pail (Fig. 1). Three screen windows increase the working surface of the pail and also prevent it from becoming too full of water. The propeller circulates water rapidly in and out of the four screen surfaces when the pail is swirled in the water.

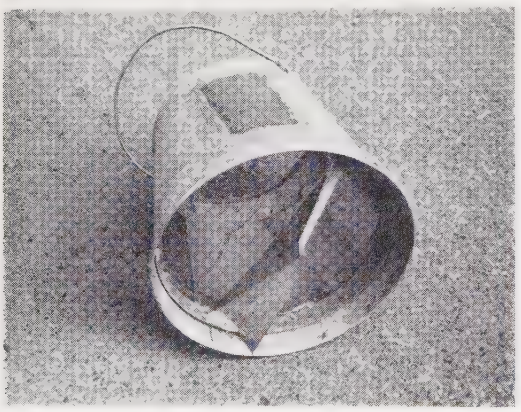

Fig. 1. Screened pail showing arrangement of stationary propeller.

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[1] Aid was received from National Science Foundation, grant G-3831. Dr. Bromfield Ridley assisted in the construction of the first model of this apparatus.

REFERENCE

Rawson, Donald S. 1953. The bottom fauna of Great Slave Lake. J. Fish. Res. Bd. Canad., **10**: 486–520.

XV International Congress of Limnology

The 15th International Congress of Limnology, a triannual meeting of SIL (Societas Internationalis Limnologiae), is to be held in North America for the first time. It will be sponsored in the United States by ASLO with the cooperation of the National Academy of Science–National Research Council, and will be held at the University of Wisconsin on 19–25 August 1962. A general announcement of the schedule and instructions for SIL members who contribute papers will be made approximately 1 April 1961. Please direct all requests concerning reservations, membership in SIL, program schedules, and other Congress activities to: XV International Congress of Limnology, c/o Dr. John C. Wright, Executive Secretary, Birge Hall, University of Wisconsin, Madison 6, Wisconsin.

Fourth Conference on Great Lakes Research

The Fourth Conference on Great Lakes Research will be held in the Rackham Building in Ann Arbor, Michigan, on April 17 and 18, 1961. The conference will be sponsored by the Great Lakes Research Division (formerly Great Lakes Research Institute) of the University of Michigan's Institute of Science and Technology. The Proceedings will be published, and inquiries regarding presentation of papers or further information may be addressed to the General Chairman, Dr. Charles F. Powers, Great Lakes Research Division, 1119 Natural Science Building, Ann Arbor.

International Association for Quaternary Research

The International Association for Quaternary Research (INQUA) will meet in Poland during the late summer of 1961. The Congress, which meets every four years, will be preceded by an excursion starting from Warsaw on August 27. The first meeting of the Congress will take place on September 2 and the last meeting on September 7. A post-Congress excursion will be held from September 7 to 21 and will visit the main localities containing Polish Quaternary deposits.

INQUA was first organized during an international geological meeting in Copenhagen in 1928 for the purpose of approaching Quaternary problems on an interdisciplinary level particularly in the fields of geology, archaeology, climatology, and chronology. Although the Congress has been attended primarily by Europeans, it is international and non-Europeans are urged to attend.

It has been the desire of many Europeans and Americans to hold the Congress in the United States sometime in the future. To this end the National Academy of Sciences—National Research Council created a U. S. Committee on INQUA. This committee is making plans to invite the next Congress to meet in this country during the late summer of 1965.

All persons interested in the 1961 Congress in Poland may obtain more detailed information by writing to the following: Professor Rajmund Galon, Secretary General, INQUA, Geographical Institute, University, Toruń, Poland.

Publications by the U. S. Atomic Energy Commission

The Division of Biology and Medicine of the U. S. Atomic Energy Commission has provided the Society with copies of two of their recent publications:

1) "Marine Sciences Research" (TID-4040, Jan. 1960) which comprises a statement on the Commission's interest in marine sciences research followed by brief descriptions of 26 projects in marine research that are currently being sponsored by the Division of Biology and Medicine.
2) "A Selected List of References on Marine and Aquatic Radiobiology" (TID-3903, May 1960) which contains 422 titles and an author index.

Members of the Society may obtain copies by remitting the cost of postage (20 cents in stamps or coin) to the Secretary-Treasurer, Dr. George H. Lauff, Marine Institute, Sapelo Island, Georgia.

BOOK REVIEWS

HYNES, H. B. N. 1960. **The Biology of Polluted Waters.** Liverpool University Press. xiv + 202 pp. Price 25 shillings ($3.50).

Pollution is fundamentally a biological problem. Yet, incongruously, many persons who have the responsibility both here and in Britain for managing pollution and studying its effects on natural waters have had little or no biological training, and consequently little appreciation of the biological processes involved. To them pollution is a chemical or an engineering problem.

Hynes' purpose in writing this book was to remedy this deficiency in understanding. Although the book is intended for the person with no previous biological training, it will also be of great use to biologists and limnologists, since it represents the best presentation to date in the English language of the biology of streams and of the changes in the biota resulting from various types and degrees of pollution.

Pollution itself is a relative term, difficult of precise definition, because many instances considered pollution in one place have their exact counterparts occurring naturally in others. Pollutants are classified into six major types, each of which has its characteristic effects upon the freshwater biota. Seldom, however, is a source of pollution of a single type, so that the reactions of the biota are complicated by interactions. In many respects the organisms furnish better evidence of pollution, especially in mild cases, than do the ordinary chemical analyses, and the occurrence and severity of pollution is generally more readily and rapidly apparent from a biological examination than from chemical analyses. Nevertheless, both lines of evidence are needed in assessing the effects of pollution. Chemists and biologists should work closely together.

Hynes discredits the use of indicator organisms as being unrealistic biologically, and the saprobic system as being a "rather clumsy tool in the actual assessment of pollution in its many and varied aspects." The organisms involved in pollution abatement all occur naturally in streams and lakes. None of them is characteristic of and confined only to polluted situations. The more elaborate system currently being used by Patrick and her co-workers is regarded as being too complicated and requiring the services of too many specialists. Independently Hynes reached the same general conclusion as the group at Cincinnati (Tarzwell, Gaufin, Katz, and Doudoroff) that changes in the abundance of the dominant stream organisms, especially the larger invertebrates, provide a readily obtainable and realistic assessment of the effects of pollution. The chief difficulty here is the sampling technique, which involves intensive collecting with a hand net for a given period of time at each station. Where one investigator does the sampling at all stations the results are comparable, but a standardization of the technique is needed to make the results of different investigators comparable. Species lists by themselves are of relatively little value; the over-all composition of the community must be known. Hynes presents a number of excellent examples from his own investigations of mild levels of pollution entirely undetectable by chemical means, and of gradual biological recovery of a stream from pollution with improvement in the methods of waste treatment.

Lakes are considered from the standpoint of the eutrophication which occurs naturally in them and which is accelerated by the addition of even well-treated effluents. Unlike streams, the pollutional effects in lakes are irreversible at the present state of our knowledge.

The greatest problem in the disposal of organic materials is the tremendous wastage involved. Fifty percent or more of the salts of nitrogen and phosphorus eliminated or excreted by man occur in the stabilized effluent of sewage disposal plants. The recovery of this material by chemical or biological means should be of major concern to human ecologists. An interesting suggestion is that even the heat of cooling water might be utilized for heating greenhouses to grow truck crops fertilized by nutrients from a nearby sewage disposal plant.

The book is timely, exceedingly well written, and authoritative. The sanitary engineer or chemist will be bothered by the names of organisms, many of which have no common names, but he can assign mental x's and y's to them. These are parts of the necessary specific language of biologists and cannot be dispensed with completely. However, the general concepts in the presentation can be appreciated and understood by the non-biologist without the necessity of having a specific organism in mind for each name mentioned. A generous supply of excellent line drawings in the book helps bridge the gap.

A book of this type has long been overdue. It should help greatly to bring more biology and biologists into the whole area of pollution and pollution abatement. We can hope that Hynes with his talents for writing and organization will tackle the even more difficult task of producing a comprehensive book on stream limnology.

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TAYLOR, W. R. 1960. **Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas.** x + 870 pp., 14 text figs., 80 pls. University of Michigan Press, Ann Arbor, and Ambassador Books Ltd., Toronto. **$19.50.**

Professor William Randolph Taylor's latest book will be useful not only in field courses but also to the professional biologist doing field work at any of the eighteen or more marine stations in the western warm Atlantic. Hopefully, it will serve as a starting point for some needed monographic work, which may be the reason for the reminder in the preface that "this is in the aggregate a pioneer work." Professor Taylor is being unnecessarily modest—his book reflects the matured judgment to be expected from unequalled field and herbarium experience during more than 30 years. Until the monographers do establish better diagnostic criteria than are now available for some algal taxa, Taylor's taxonomic opinions will merit the users' confidence.

Judging from reactions at Hawaii, two aspects of the book may excite immediate comment: first, the illustrations; second, the price. There are 14 full-page photographs illustrating the introductory material on algal habitats and 80 plates of drawings and photographs in support of the systematic list. Five persons in addition to the author are given credit for these plates. The drawings are all clear and skillfully executed (these are no simple student drawings, be it noted!) but in particular some of those by E. A. Salgado are worth special mention. This reviewer knows of no other modern book on algae which is so handsomely and thoroughly illustrated.

The matter of price points up the irony that more than one phycologist was willing to pay this much or more for Taylor's earlier work on the Florida algae during the years when it was out-of-print, yet the present book is more nearly complete, better illustrated, and more mature but will probably be considered too expensive by many who need it (until it too is out-of-print?). Be that as it may, it must be conceded that the price will undoubtedly restrict the sales of the book.

For those whom the price restricts to merely an entry in their card indices, the following information may be useful: Geographical range—roughly from 32°N to 27°S, comprising Bermuda and the United States coast southward from North Carolina, the Gulf of Mexico, Central America and the Caribbean, Venezuela, the Guianas, and Brazil; Taxonomic range—mainly Chlorophyceae, Phaeophyceae, and Rhodophyceae (Cyanophyceae and Bacillariophyceae are omitted, but one species each of Cryptophyceae and Chrysophyceae are included plus the genus *Vaucheria* in the Xanthophyceae) for a total of 760 species; New combinations—transfers to *Phaeophila*, *Entocladia*, *Pringsheimiella*, *Herponema*, *Giffordia*, *Padina*, *Hecatonema*, *Gelidiopsis*, *Fosliella*, *Antithamnion*, and *Hymenena*, and a transfer within *Caulerpa*; New taxa—the family Wurdemanniaceae, new species in *Caulerpa*, *Dictyota*, *Dictyopteris*, *Padina*, *Cryptonemia*, and *Ceramium*, and new varieties in *Dictyota*, *Galaxaura*, *Rhodymenia*, and *Herposiphonia*.

Even if the price of the book militates against heavy sales, its versatility should not, for there is much in it for the beginner as well as the professional. Graduate students interested in smaller portions of the range will find the bibliography (338 entries) and the historical treatment in the introduction as valuable as will the monographer and nomenclaturist who want to track down original reports. For the novice collector there is a section on field work and on algal habitats, the latter being also of use to descriptive ecologists. In the section on algal habitats, incidentally, the author does a convincing job of dispelling the notion "that few seaweeds, and these Rhodophyceae, go down to more than a few meters depth." The systematic portion contains descriptions of taxa from orders down and is immeasurably more useful than a mere floristic list. The treatment seems to have been conservative, and some who have been brought up on American textbooks may disapprove of the absence of names of divisions or phyla, and the limits ascribed to some of the orders. On the other hand it is a relief to note that no new species are proposed in *Cladophora* and *Enteromorpha*, either! As with Dr. Taylor's other books, there is no general key. The beginner may find this annoying, although it is doubtful whether a beginner could handle a general key to a flora of this size, and he will have to thumb through the illustrations until he gets something of a "feel" for the families and genera. Keys to families, genera, and species are distributed through the descriptive catalogue. The two or three which were followed through by the reviewer seemed clear and workable.

Inevitably, a work of this size presents opportunity for quibbles or questions. One notes with surprise, for instance, that *Valonia ventricosa* is reported for Bermula, since to this reviewer's knowledge it has not been found there recently and older records were presumed to confuse it with *Halicystis osterhoutii*. It is also surprising that no comment is made either under *Halicystis* or *Derbesia* concerning the evidence linking the life cycles of some species of these genera. The problem is especially interesting in the region under consideration since it harbors only one species of *Halicystis*, and that without a known alternate phase, but three species of *Derbesia* are present, of which *D. marina* has been experimentally shown to have a "Halicystis phase." Similarly, there is no mention that cultures show *Porphyra umbilicalis* and *Bangia fuscopurpurea* to have stages identifiable with *Conchocelis rosea*, which seems to be absent from this flora. On the other hand, the linkage of life cycles between *Falkenbergia* and *Asparagopsis* is acknowledged with the comment that experimental confirmation is lacking for the species at hand. A few inadvertencies

were detected: Castellanos 1945 is cited on page 2 and Hollenberg 1935 on page 109, but they were left out of the bibliography. Humm's rediscovery of *Anadyomene menziesii* (Bull. Mar. Sci. Gulf Carib. 6: 346–348, 1956) may have been reported too late for inclusion but it is unfortunate that his earlier work (A collection of marine algae from Guantanamo Bay, Cuba. *Ibid.*, 5: 240–246, 1955) is not mentioned, since it includes 18 species that Taylor does not record for Cuba. Of these, *Aglaozonia canariensis* will especially need confirmation because all previous reports in this range turned out to be *Pocockiella variegata*, and *Ulothrix subflaccida* should also be confirmed because it represents an addition to the whole region. The only other inadvertencies noted were some misspellings. In the index and on page 489 *Chylocladia rigens* and *Cordylecladia rigens* are misspelled as is *Dipterosiphonia rigens* on page 601. The misspelling of *Acicularia schenckii* on page 107 is probably a typographical error, since it is given correctly in the index. These are not criticisms which detract significantly from the merits of the book and the reviewer offers them mainly to show that he has worked for his sixpence.

The only serious complaint is that an ordinary machine casing instead of a library binding was used and it does not seem adequate for a book of this thickness. Broken spines and loose hinges are sure to result if the book is handled too casually. Editorially and typographically the book is excellent. The layout is designed to make the text easy to follow and headings are effectively used. There was no scrimping of space in the bibliography, so citations including full pagination, figures, and plates were possible. The quality of paper and reproduction gives full justice to the illustrators' labors. All told, the book is well worth the price.

A. J. Bernatowicz

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Yonge, C. M. 1960. **Oysters.** A New Naturalist Special Volume. xiv + 209 pp. Collins Clear-type Press, London. 21 shillings (= approx. $3.10).

This New Naturalist Monograph was originally intended to be an account of the European flat oyster, *Ostrea edulis*, but because of the necessity to refer to literature on other oysters in order to explain some points in the biology of *O. edulis*, the author found himself compelled to write on oysters in general. Not only are these molluscs of considerable popular interest and commercial value, but as the author says, "Probably no marine animals—and certainly no marine invertebrates—have been so intensively studied and we are no more than at the beginning of intimate knowledge about them."

The topics covered are, first, a very brief account of the probable origin and evolution of oysters, sessile bivalve molluscs so specialized that they have lost both "head" and "foot." Then, a description of *O. edulis* in detail and a few comparisons with other oysters, an account of reproduction and development also centered on *O. edulis* with some information on other forms, a discussion of the species of oysters and their distribution, a general account of life and habits of various kinds of oysters, a chapter on enemies, competitors, and diseases, one on fossil oysters and on oysters in human history and prehistory ("oysters in the past"), and finally a long and very interesting chapter on oyster culture.

As is fitting in a book intended for a wide audience, this little "monograph" is written in a breezy journalistic style (but without any nonsense) and should be easy reading. However, one sometimes has the impression that it was "dictated but not read," and that it would be much easier reading if the writing had been more difficult. Many sentences have such a confusing structure that they must be read twice; all of these could have been made clear and easy reading by a little more effort in rewriting. There are very few misprints, and these few are not apt to be misleading.

There is a tremendous lot of good sound information packed in the 194 text pages, so much that even a professional oyster biologist is sure to learn here some things he did not know before. The author has done a remarkable job of including the very latest information before the book went to press. Practically no outright errors of fact were noted, but some statements on American conditions are a little misleading. Even though Dr. Yonge has spent much time in North America, he could not be expected to know the country like a native. The statement on p. 117, "Damage . . . exceeding one million dollars has been done in a single year to the oyster beds in Long Island Sound and there are few areas where starfish are not a major pest," is ambiguous. There may be few areas in Long Island Sound where starfish do not prey on oysters, but outside of the Sound there are few places on the Atlantic or Gulf coast where starfish normally occur on oyster beds. *Crassostrea virginica* does not "range extensively off Atlantic coasts" as stated on p. 85, but is normally confined to estuaries, bays, and sounds. It did not even occur in the deep open waters of Long Island Sound until it was planted there, and it can be maintained in these waters only by replanting and by a constant war against predators.

On enemies, competitors, and diseases, there was a large mass of very recent literature to be digested quickly, just before going to press, so it is not surprising that a few errors crept in. It is not known to be true, as stated on p. 124, that the parasite fungus *Dermocystidium marinum* is spread largely by crabs; however, this statement was made in a review published by an American biologist, so Yonge's mistake is excusable.

Menzel and Hopkins (1955) noted that a single oyster infected by *Bucephalus cucullus* grew unusually fast and suggested that parasitic castration

might cause this effect in oysters, as in snails, but did not claim to have proved this as implied on p. 122. Similarly, the statements implying that *Hexamita* infection was the cause of widespread mortalities of oysters in Europe and Canada, on pp. 124 and 158, are stronger than those made by the original authors (Mackin, Korringa, and Hopkins, 1952).

There have been books about oysters before, several of which are listed among Yonge's 93 selected references. Only eight years ago, Korringa reviewed all recent advances in oyster biology up to about 1951. Yonge's book shows that there have been important advances on knowledge of oyster biology, especially on knowledge of oyster diseases, even since 1951. This book will give aquatic biologists a chance to get a quick review of what is now known about oysters. It would make a valuable and inexpensive addition to one's private library.

SEWELL H. HOPKINS
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PROCEEDINGS OF THE AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY, INC.

23RD ANNUAL MEETING
STILLWATER, OKLAHOMA
AUGUST 30, 1960

The meeting was called to order by President B. H. Ketchum at 11:17 A.M.; 76 members were present. The minutes of the 22nd annual meeting were approved as printed in LIMNOLOGY AND OCEANOGRAPHY, Volume 5, Number 1.

In the President's report, Dr. Ketchum reviewed the special committees that had been appointed for the purpose of planning and organizing the XV Congress of the International Society of Limnology, to be held in Madison, Wisconsin in 1962. Dr. A. D. Hasler is the General Chairman; the committees already appointed are as follows:

Executive Committee:
A. D. Hasler, Chairman
D. G. Frey
G. H. Lauff
D. S. Rawson

Advisory Committee:
W. E. Ricker
R. W. Pennak
R. S. Rawson
D. G. Frey
F. E. Fry
T. T. Macan
G. H. Lauff
E. S. Deevey
R. W. Hiatt
B. H. Ketchum
G. Sprugel
S. Galler
A. D. Hasler

Program Committee:
D. G. Frey, Chairman
W. T. Edmondson
R. C. Ball
F. R. Hayes
J. R. Vallentyne
C. M. Tarzwell

U. S. Representative to SIL Grants Committee:
W. T. Edmondson

Canadian Representative to SIL Grants Committee:
F. R. Hayes, Chairman
W. E. Ricker

Committee on Excursions:
K. B. Carlander, Chairman

Finance Committee:
G. H. Lauff, Chairman

Committee on Funding of Excursions and Fellowships:
J. R. Olive, Chairman

Committee on Transportation:
S. R. Galler

A new standing committee on Education and Recruitment was appointed, following the instructions of the membership at the 22nd annual meeting. The membership of the committee is as follows:

A. C. Redfield, Chairman
R. Arthur
J. C. Ayers
C. A. Barnes
A. D. Hasler
D. W. Hood
F. Koczy
D. W. Pritchard
B. H. Ketchum (*ex officio*)

Consultants: G. A. Riley
M. B. Schaefer

Appointments made to other standing committees during the past year are as follows (last year of each individual's term of office is indicated):

Identification Committee:
J. L. Brooks (1962)

Apparatus and Supply Committee:
J. H. Ryther (1962)

Additional special committee appointments were as follows:

Auditing Committee:
J. C. Ayers (1960) D. C. Chandler (1960)

Nominating Committee:
W. E. Ricker, Chairman (1960) M. C. Sargent (1960)
G. L. Pickard (1960) R. W. Pennak (1960)

Tellers:
K. W. Cummins (1960) J. C. Ayers (1960)
M. Parker (1960)

Cooperative Ship Committee: (extended through 1961)
H. T. Odum, Chairman G. Gunter
F. G. Walton Smith D. F. Leipper
S. Fox

The President discussed the role of special meetings to emphasize the problems of physical oceanography and to attract more of that group to membership in the Society. The special meeting held with the Pacific Division of the Society in June, 1960, drew few new attendants beyond the Division's regular membership. The need of independent meetings, away from the distractions of competing societies and programs was noted; the matter was discussed by the Board of Directors and their recommendations are presented below.

The report of the Secretary-Treasurer was presented by Dr. G. H. Lauff. It was reported that during 1959–60 (since the last report), 126 members had joined the Society, of whom 122 are active members and 4 are associates. During the same period, 7 active members resigned and 20 were dropped from membership for nonpayment of dues. Three members died during the past year.

The total paid membership, as of August 22, 1960, was 984, of whom 22 are associate members and 14 are emeritus members. The number of members subscribing to the journal has increased to 948, which compares with 833 subscribing members one year ago. There were 401 nonmember subscriptions (352 subscribers) to LIMNOLOGY AND OCEANOGRAPHY during the past year. The total number of nonmember subscriptions had changed from 298, representing an increase of 103.

The results of the election of officers for 1960–61 were reported as follows:

President	W. T. Edmondson
Vice-President	G. A. Riley
Member-at-Large (3-year term)	F. R. Hayes
Editorial Board (3-year term)	R. O. Reid, G. R. Rounsefell, J. Verduin

It was reported that the Internal Revenue Service, U. S. Treasury Department, has granted the Society a "tax exempt" status after appropriate amendment of its Articles of Incorporation demonstrated that it was organized and operated exclusively for educational and scientific purposes.

The report of the Secretary-Treasurer was approved as presented. The more favorable conditions of journal publication during 1960 were reviewed and it was indicated that a generally improved financial status could be expected. Dr. K. M. Rae, Editor, discussed the backlog of manuscripts for publication in LIMNOLOGY AND OCEANOGRAPHY and indicated that a waiting period of 8–10 months could be anticipated. The publication of the various numbers is proceeding on schedule; the operational arrangements with The Allen Press have been very satisfactory.

Dr. A. C. Redfield, Chairman of the Committee on Education and Recruitment, presented the report prepared by his committee. The committee and its activities were initiated in recognition of the Society's responsibilities in connection with the education of additional personnel required by the expansion of all fields of oceanography as envisaged by the Committee on Oceanography of the National Academy of Sciences.

After comments from the floor, it was agreed that the title and other editorial corrections noted would be made prior to the submission of the report for publication in LIMNOLOGY AND OCEANOGRAPHY. It is anticipated that reprints will be available so that the information can be utilized in counselling in high schools and colleges, as well as providing sufficient copies for extensive distribution to interested agencies and institutions. The value of a similar report for counselling students in other areas of aquatic biology was recognized. The report was accepted, and the committee commended for its worthy contribution.

Dr. A. D. Hasler, general chairman for the planning and organization of the International Congress of Limnology, reviewed the status of finances for the 1962 meeting in Madison and provided details on the operation and activities of the various subcommittees. A preliminary budget of $100,000 has been established and a major portion of the funds has already been derived from federal agencies. It is expected that additional funds must be obtained to support some of the excursions and other activities planned.

The Cooperative Ship Committee for the Gulf Coast Area, under the chairmanship of Dr. H. T. Odum, is in the process of appraising the need for a "pure science" ship and will provide suggestions on methods of financing, mechanics of scheduling and related problems. A questionnaire on these matters will be circulated.

Dr. B. H. Ketchum, Chairman of the Joint Committee in Aquatic Biology (Ecological Society of America and ASLO), reported that the group had voted to establish a section on Aquatic Ecology within the Ecological Society of America. It is hoped that future ASLO programs may be planned with this group to eliminate the separation of interests and the duplication of effort.

The reports of other standing committees and of representatives were briefly reviewed and added to the Society's records.

The President reported that the Board of Directors had recommended that the 1961 meeting at Purdue University be a program meeting with AIBS and its affiliate organizations. To assist in attracting a larger contingent of oceanographers and related scientists to the Society, the Board further recommended that the Woods Hole Oceanographic Institution be approached to ascertain the likelihood of holding the next annual business meeting at Woods Hole, Massachusetts during early September, 1961.

It was the opinion of the Board of Directors that the Society's meetings with AIBS and its affiliates should continue, but that a series of special meetings should be arranged to promote interest in oceanography, and offer the promise of attracting scientists who are not now members. The locations and areas considered were as follows: Woods Hole, Miami, Texas and/or Texas A&M, Scripps, University of Washington, Canada (British Columbia or Dalhousie) and the Great Lakes (Michigan).

The discussion that followed the announcement of the next annual meeting pointed out that the Society has many other interests beyond those represented by its AIBS affiliates. It was suggested that continued regular meeting with AIBS was perhaps unfair to the over-all ASLO membership, and functioned in hindering the growth and development of a strong, broad program. Some felt that the recommendations of the Board would fragment the Society, but there was general agreement on the need for representation of all facets of the sciences within the Society membership. A membership vote terminated discussion on this subject. Dr. Ketchum will initiate communication with the Woods Hole Oceanographic Institution regarding the 1961 annual meeting.

The rapid rise in subscriptions to LIMNOLOGY AND OCEANOGRAPHY during the past three years may necessitate another increase in the press run during 1961—it was increased from 1,000 copies to 1,500 in 1958. The Secretary-Treasurer was authorized to increase the number of copies printed "up to 2,000" on the recommendation of the Board of Directors.

Costs of reprinting Volumes I and II of LIMNOLOGY AND OCEANOGRAPHY were presented and the Secretary-Treasurer was authorized to reprint these numbers if a detailed investigation indicated that the Society's financial status will permit such expenditures. Requests for these out-of-print volumes will provide over $1,000.00 from immediate sales, and should represent over 50% of the anticipated expenditure.

A brief discussion of the production costs of Volumes I–V of LIMNOLOGY AND OCEANOGRAPHY disclosed that the Society's present policy of charging new members for back volumes at the rate of $7.50 was not valid. The meeting moved that effective January 1, 1961, all available back volumes may be purchased at the rate of $10.00 per volume.

The names of Drs. D. G. Frey and F. F. Koczy are to be submitted to the National Academy of Sciences, as the Society's nominees for the official delegation to the Congress of the International Association of Quaternary Research (INQUA) to be held in Poland during the summer of 1961.

The meeting moved that the Society approach AIBS on the translation and publication of two Russian monographs, *Primary Productivity of Water Basins* by Georgii C. Vinberg and *Foundation of the Biological Productivity of Waters* by G. S. Karzinkin. The Secretary was directed to initiate an appropriate request.

Other items of new business including the proposed budget were deferred because of time limitations, but will be discussed and resolved through communication with the Board of Directors.

A vote of thanks was extended to Dr. T. C. Dorris, local chairman for the meeting at Stillwater, and to Dr. G. W. Prescott for the preparation of an interesting and informative program.

The meeting was adjourned at 12:57 P.M.

Respectfully submitted,
GEORGE H. LAUFF
Secretary-Treasurer

Income and Expense Statement
January 1–December 31, 1959

Society

Income			
Dues Collected in 1959	$ 2,718.17		
Interest	421.13		
Special Publications	25.65		
Miscellaneous	10.50	$ 3,175.45	
Expense			
Addressing and Mailing	$ 19.63		
Printing	312.44		
Postage	286.52		
Secretarial	752.69		
Miscellaneous	255.94	1,627.22	$ 1,548.23 cr.

Journal

Income			
Volume I	$ 401.72[1]		
Volume II	402.39[1]		
Volume III	388.75[1]		
Volume IV	6,577.25[1]		
Reprints	1,491.94		
NSF Payment toward Vol. III publication deficit	2,570.80		
Miscellaneous (charges for excess material)	417.04	$12,249.89	
Expense			
Manufacture	$11,360.60[2]		
Addressing and Mailing	285.63		
Reprints	1,477.78		
Editorial	98.70		
Miscellaneous (travel; insurance bond)	386.03	13,608.74	1,358.85[3] dr.
			$ 189.38

[1] Pro-rated cost of manufacture of Volumes I–IV sold during 1959 was $9,345.02, as compared to receipts of $7,770.11.

[2] Based on the pro-rate cost of manufacture, Volume IV inventory represents an asset of $2,652.06.

[3] Deficit for 1959 Journal operation, excluding the NSF payment for Vol. III (1958), was $3,929.65.

Balance Sheet
December 31, 1959

Assets		*Liabilities*	
Cash	$ 4,187.98	Accounts payable	$ 2,037.50
Accounts receivable	974.23	*Equity*	
Inventory	5,906.46	Earned surplus	9,031.17
	$11,068.67		$11,068.67